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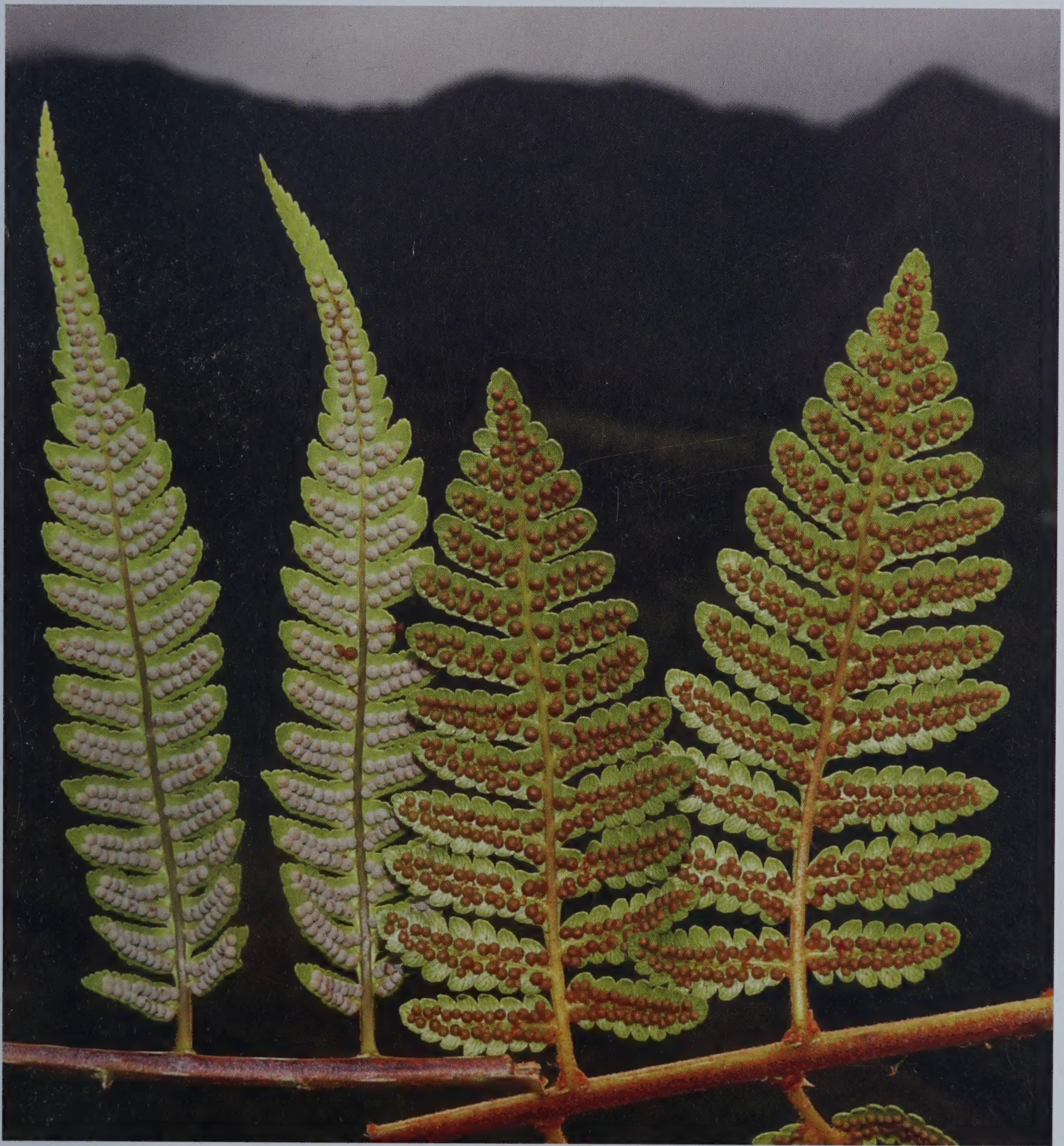

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Six New Scaly Tree Ferns (*Cyathea*: Cyatheaceae) from Northern Peru

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Abstract.—On the basis of recent fieldwork, six new species of *Cyathea* from northern Peru are described: *Cyathea carolinae, C. cisandina, C. grata, C. oscarorum, C. phoenix,* and *C. novoi.* All were found on sandstone subtrates under different precipitation regimes. Here, we illustrate these species, discuss their natural history, compare them to their putative close relatives, and discuss the implications of their discovery for the floristics of South American tree ferns.

Key Words.—Amotape-Huancabamba, Andes, Neotropics, sandstone, South America

The scaly tree ferns (Cyatheaceae) comprise an estimated 643 species in 4 genera and constitute the most diverse clade of tree ferns within the Cyatheales (PPG 1, 2016; Dong and Zuo, 2018). Because of their usually large size, radial crowns, and abundance, scaly tree ferns are conspicuous elements in humid, tropical montane and southern temperate forests (Braggins and Large, 2004). Many tree ferns, however, are small species of the forest understory, exposed rocky faces, or nutrient poor soils such as those that develop on sandstones and white sands, and could be mistaken for non-tree ferns by generalist collectors. The last two decades has seen an increase in the rate of description of new scaly tree fern taxa from the Neotropics, many of them small or dwarf species discovered in sandstone substrates of the equatorial and subequatorial Andes (e.g., Lehnert, 2003, 2006, 2008, 2009, 2011a; 2016; Lehnert and Tejedor, 2016; León and Moran, 1996; Moran, 1991; Rojas and Tejedor, 2016; Smith, 2006; Tejedor and Calatayud, 2017; Tejedor et al., 2017). This surge in species descriptions led some authors (Lehnert and Tejedor, 2016; Tejedor and Calatayud, 2017 a, b) to suggest that additional new species of small tree ferns should be discovered through further collections in little-explored Andean ridges and plateaus. This prediction has been supported by the recent description of the dwarf tree fern *Cyathea leoniae* Acuña-Tarazona & Huamán-Melo (Acuña-Tarazona et al., 2018) from a sandstone mountain in San Martín, northern Peru, and is further confirmed by the present study. Here, we describe six more species of small tree ferns from white sands or sandstone outcrops also in the northern Peruvian Andes. We illustrate each species, compare them with similar species, include observations on their natural history, and discuss the implications of our findings for understanding the floristics of tree ferns in South America.

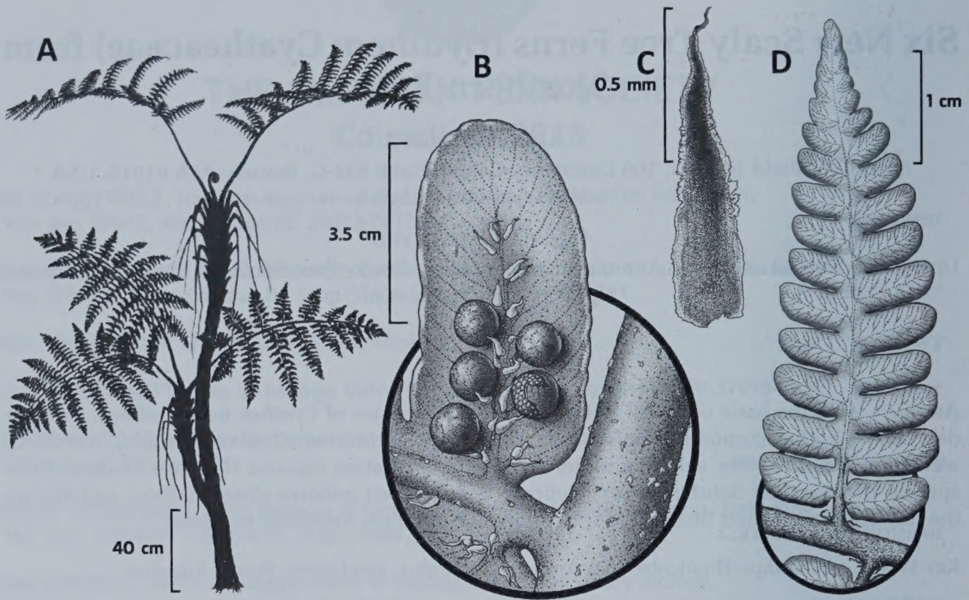

FIG. 1. *Cyathea carolinae.* **A.** Habit. **B.** Fertile segment abaxially. **C.** Petiole scale. **D.** Fertile pinnule adaxially (drawn from G. Calatayud 6096 USM, CUZ).

MATERIALS AND METHODS

Field trips in Peru were completed between October 2017 and March 2018. Comparative material was studied at the herbaria HOXA, NY, and USM and online resources were used for checking type specimens (plants.jstor.org) and historic literature (www.biodiversitylibrary.org). Barcodes are not available at the herbaria visited. Terminology follows Lellinger (2002) and Lehnert (2011b). Line drawings were made by Sylvia Gutierrez with pen and ink and by the first author using Adobe Photoshop.

TAXONOMIC TREATMENT

Cyathea carolinae A. Tejedor & G. Calatayud, **sp. nov.** Type: PERU. Amazonas: Pomacochas, trocha a San Lorenzo, -5.7874, -77.9909, 2800 m, 15 Oct 2017, *G. Calatayud* 6096 (holotype: USM! isotypes: CUZ! HOXA!). Fig. 1.

Diagnosis.—Resembling *Cyathea hierbabuena* A. Tejedor and G. Calatayud but differing in its markedly erose scale margins, abundant bullate cream squamules along main veins abaxially, stalked pinnules, glabrous axes abaxially, glabrous lamina adaxially, and more gracile, sometimes multi-stemmed habit.

Trunks to 1.5 m tall, slender, 4–5 cm diam., erect, inermous, retaining old petiole bases, covered in scales similar to those of petioles; apices hidden by a tight fascicle of petiole bases; often with adventitious buds along trunk length. Fronds to 1 m long, patent from ascending petioles. Petioles to 30 cm long, sparsely verrucate, epidermis matte olive green adaxially, shiny bright green abaxially in life, very sparsely scurfy, scurf consisting of twisted whitish-cream, lanceolate squamules to 1 mm long and irregular, highly dissected cream squamules to 0.5 mm diam.; petioles scaly abaxially along basal half to 2/3 of their length. Petiole scales lanceolate, to 15 × 3 mm, bases cuneate to truncate, apices acute to attenuate, straight to wavy or falcate, flat; bicolorous with orange brown to dark brown centers and paler orange brown margins; differentiated margins broad, without setae, markedly erose. Laminae to 48–50 × 36–38 cm, ovate, bipinnate-pinnatisect, soft herbaceous, shiny bright green adaxially, paler abaxially; apices gradually reduced. Rhachises sparsely verrucate abaxially, matte olive green adaxially, shiny bright green abaxially in life; adaxially hairy with yellowish to brown acicular, translucent, antrorsely appressed, thick multicellular hairs to 0.5 mm long. Pinnae to 19 cm long, short-stalked to 5 mm, ca. 7–8 pairs per frond, patent to weakly ascending, alternate, inarticulate, ovate lanceolate, distal segments weakly decurrently adnate before ending in a pinnatifid apical section; basal pinna pairs about ½ the length of medial pinnae, reflexed. Costae to 1 mm wide, inermous, matte olive green adaxially, shiny bright green abaxially in life, alate along distal 1/3, epidermis adaxially obscured by dense indument similar to that on rachises, abaxially with cream twisted ovate-lanceolate squamules to 0.5 mm long with caudate twisted tips; insertion of costae and rachises adaxially often with caduceous linear brown squamules to 2.5 mm long; junctures weakly swollen abaxially, each bearing a slightly swollen elliptical pneumathode to 1 mm diam. cream to pale brown. Pinnules lanceolate triangular to 40 × 14 mm. Costules to 0.3 mm wide, olive green adaxially and bright green abaxially in life, adaxially covered by dense indument similar to that on rachises, abaxially with many cream to pale brown, bullate squamules to 0.5 mm long with caudate tips, and brown flat lanceolate to ovate squamules to 1.5 mm long with attenuate twisted tips. Largest segments 5–6 × 3 mm, segments patent to weakly ascending, oblong, tips obtuse to rounded, sinuses acute, to 0.5 mm wide; segments subopposite to alternate, proximal segments larger than medial segments, nearly remote on proximal pinnules; margins usually entire, rarely crenate; veins green in life, glabrous, sunken adaxially, flat abaxially; sterile and fertile veins usually forked, rarely simple; midveins abaxially covered with many cream bullate squamules 0.5 mm, with twisted, caudate tips. Sori 1.0 mm diam., proximal, parallel to midveins, in fork of veins; indusia sphaeropteroid, thin, translucent brown, usually with a well-developed umbo, receptacles and paraphyses not examined. Spores not examined.

Etymology.—The specific epithet honors Carolina Shorter, dear friend and unfailing supporter of tree fern research and beyond.

Distribution, habitat, and similar species.—Known only from the type locality; 2750–2800 m. It grows in numbers within patches of dwarf forest in a matrix of scrubby vegetation over wet, loose white sandstone and white sands rich in humus. This peculiar habitat has a much wider extension within Cordillera de Colán, and it is likely that the species will be found in neighboring localities.

Cyathea carolinae grows with *C. hierbabuena* and *C. parvifolia* Sodiro, two species of similar stature, scale coloration, and general appearance. It could also be confused with small individuals of the more widespread *C. lindeniana* C. Presl, and *C. squamipes* H. Karst, which are also common on sandstone and may co-occur with *C. carolinae*. *Cyathea patens* H. Karst and the allopatric *C. herzogii* Rosenst., known from central Peru to Bolivia, are also similar. From nearly all of these species *C. carolinae* can be easily distinguished by its nearly glabrous lamina adaxially. The potentially confusable species, with the exception of *C. lindeniana*, all have the lamina with different degrees of hairiness adaxially, either along veins or both along and between the veins but never glabrous. From *C. lindeniana*, *C. carolinae* can be distinguished by its more compact, ovate frond, nearly scurfless axes abaxially and bright olive green axes adaxially. *Cyathea lindeniana*, in contrast, has lax, ovate-lanceolate fronds, brown scurf along axes abaxially, and dark, nearly atropurpureous axes adaxially.

Of all potentially confusable species, *Cyathea carolinae* is most similar in the field to *C. hierbabuena*, especially because both share distinctively rich orange brown bicolorous petiole scale with a dark brown shiny apex (Figure 1 C). In addition to its nearly glabrous lamina adaxially, *C. carolinae* can be distinguished from *C. hierbabuena* by its abundant cream-colored bullate squamules along the main veins abaxially, stalked pinnules, glabrous axes abaxially, and more erose scale margins. In contrast, *C. hierbabuena* has orange brown bullate squamules along costules and veins abaxially, sessile pinnules, pubescent axes abaxially, and usually entire scale margins. Also, *C. carolinae* tends to be smaller (trunks to 5 cm diam.), with greener axes and lamina adaxially, and it regularly buds along trunks, sometimes producing multi-stemmed plants. *Cyathea hierbabuena* on the other hand can attain larger sizes (trunks to 7 cm diam.), has more orange brown axes adaxially due to the dense indument of brown to orange brown hairs and linear squamules, grayish green lamina adaxially, and it has never been observed producing adventitious buds or forming multi-stemmed plants.

Cyathea cisandina A. Tejedor & G. Calatayud, **sp. nov.** Type: PERU. Amazonas: Alto Nieva, trocha a lo largo de quebrada, -5.6647, -77.7778, 1880 m, 28 Feb 2018, *G. Calatayud* 6254 (holotype: USM!; isotypes: CUZ! HOXA!). Fig. 3.

Diagnosis.—Resembling *Cyathea brunnescens* (Barrington) R. C. Moran but differing in its densely hirsute axes both adaxially and abaxially, decurrent fronds, and its distribution at higher elevations.

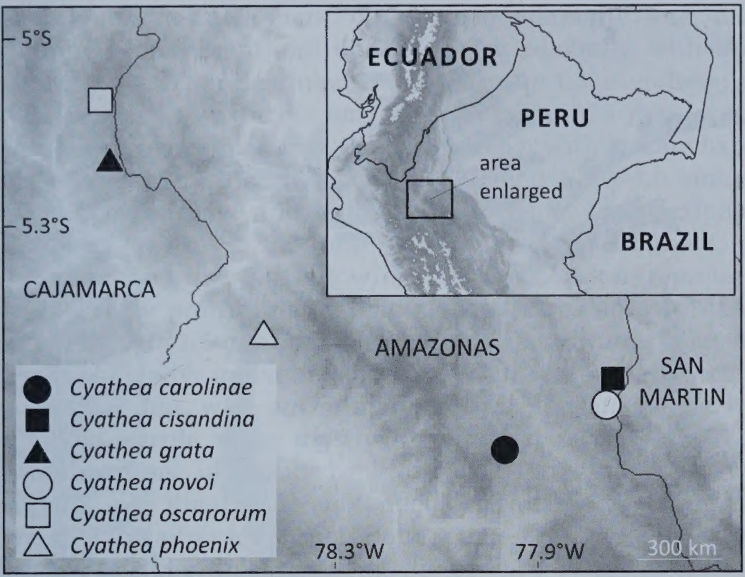

FIG. 2. Geographic distribution of six new tree ferns from Peru.

Trunks to 2 m tall, slender, 4–5 cm diam., not spiny, without old petiole bases; apices hidden by fascicles of petioles; without adventitious buds. Fronds to 150 cm long, patent to weakly arching from ascending petioles. Petioles short, to 15 cm long, armed with short spines to 2 mm, epidermis dark reddish brown to atropurpureous, shiny, scurf thick, consisting of appressed orange brown highly dissected to arachnoid squamules to 1.5 mm long; petioles scaly abaxially from base past the basal pinnae and into the rhachises. Petiole scales ovate-lanceolate to lanceolate, to 25 × 5 mm, bases round, pseudopeltately to peltately attached, apices attenuate, strongly falcate, flat to slightly wavy or sinuous; slightly bicolorous, dark reddish brown with paler orange brown, slightly translucent margins, bases atropurpureous; differentiated margins narrow, without setae, erose-dentate, fragile, often partially abraded. Laminae to 130 × 70 cm, broad-elliptic, base strongly decurrent, bipinnate-pinnatifid, firm herbaceous, rich-green adaxially, pale gray-green abaxially; apices abruptly reduced. Rhachises inermous, densely verrucate abaxially, weakly shiny, dark reddish brown to atropurpureous abaxially, and dark olive green adaxially; adaxially densely hairy with reddish brown to translucent orange, erect to tortuous, thick multicellular hairs to 1.5 mm long, with tips antrorsely curved, intergraded with erect, wavy lanceolate light orange brown squamules, most commonly at insertions with costae, abaxially and on the sides with thinner translucent brown to tan erect to tortuous hairs to 1.5 mm long. Pinnae to 40 cm long, subsessile to short-stalked to 5 mm, ca. 13–15 pairs per frond, weakly ascending, alternate, inarticulate, narrowly green-alate along most of its length, distal segments weakly decurrently adnate before ending in a pinnatifid apical section; basal pinna

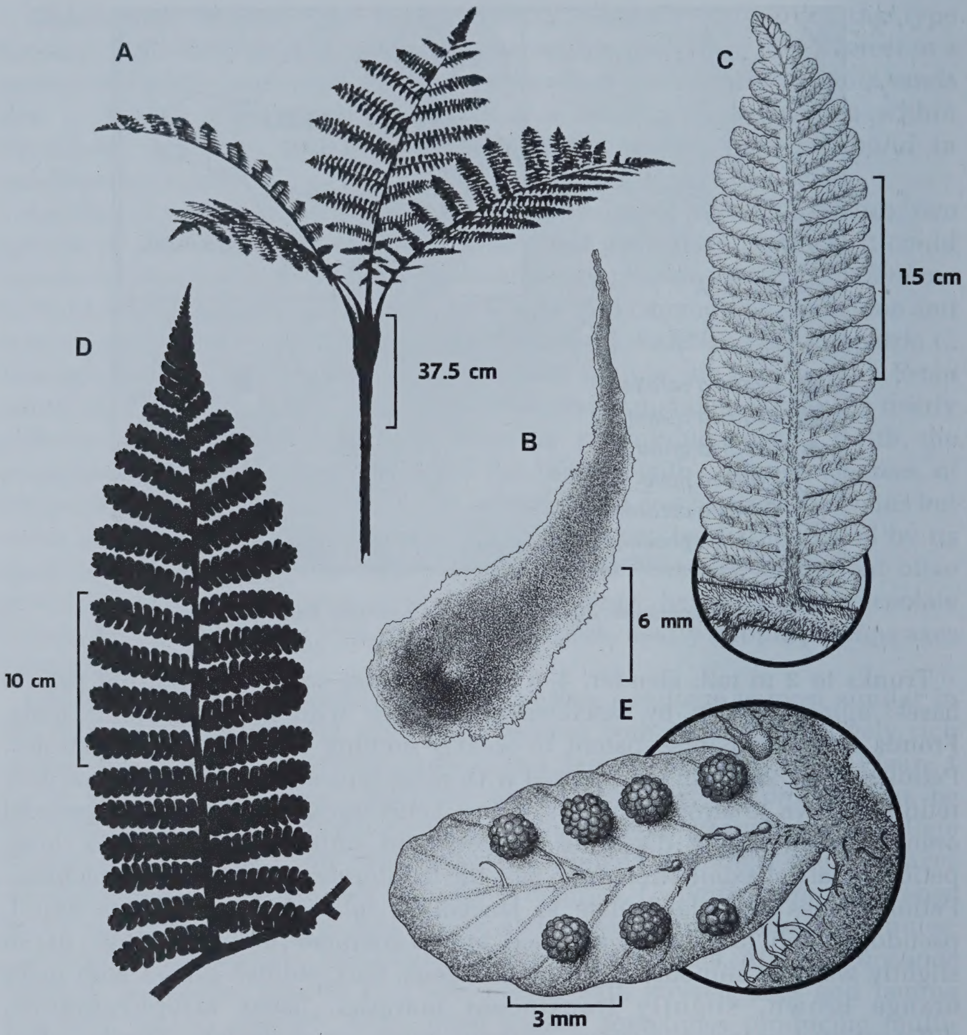

FIG. 3. *Cyathea cisandina.* **A.** Habit. **B.** Petiole scale. **C.** Fertile pinnule adaxially. **D.** Pinnae, silhouette. **E.** Fertile segment abaxially. (drawn from G. Calatayud 6254 USM, CUZ)

pairs ca. 1/5 the length of the medial pinnae, weakly reflexed. Costae to 4 mm wide, inermous, verrucate, dark reddish brown to atropurpureous abaxially, dark olive green adaxially, epidermis obscured by dense indument similar to that on rachises; junctures of costae and rachises often with a higher concentration of erect, tortuous, lanceolate pale orange brown squamules; junctures weakly swollen abaxially, each bearing a planar round pneumathode to 3 mm diam., dark reddish brown, with an adjacent conspicuous green spot in fresh specimens. Largest pinnules 50–60 × 15–20 mm, pinnules sessile, inarticulate, ca. 1.5 cm between the stalks/costules, oblong, bases truncate, inequilateral, distal segment 1/3 longer than proximal, apices obtuse to broadly acuminate; costules dark olive green adaxially and dark green abaxially, strongly prominent and densely hairy adaxially with translucent orange to tan, curved multicellular thick hairs to 1.5 mm long; abaxially prominent, with many translucent tan, tortuous hairs, to 1 mm long, and few lanceolate orange brown squamules to 1.5 mm long, with bullate bases, entire margins and attenuate tips. Largest segments 8.0–9.0 × 3.0–4.0 mm, segments patent to weakly ascending, straight to distally slightly falcate, tips obtuse to rounded, sinuses acute, $<$ 0.5 mm wide; segments alternate, proximal segments ± the same size as following segments, never remote; margins crenate; veins weakly protruding on both sides, dark green, with thick, erect, translucent tan hairs to 1.5 mm adaxially and thinner, tortuous, translucent tan hairs to 1 mm abaxially; midveins abaxially with few bullate orange brown squamules 1.0–0.5 mm, with entire margins and elongate tips; sterile veins simple or forked, fertile veins mostly forked. Sori 1.0 mm diam., medial, parallel to the margins, in fork or back of veins; indusia absent, receptacles globose, 0.2–0.3 mm diam., not subtended by squamules, paraphyses few, shorter than sporangia to ca. 0.2 mm long. Spores not examined.

Etymology.—From the distribution of the species on the Amazonian (cis-Andean) side of the Andes, whereas all putative closest relatives occur on the Pacific (trans-Andean) side of the Andes and seem to belong to a species group ancestral to the Chocó biogeographic region.

Distribution, habitat, and similar species.—Headwaters of the Nieva river in Amazonas, northern Peru, in the understory of wet montane forest very rich in tree ferns (30 species found there to date).

Cyathea cisandina is superficially similar to two sympatric species, *Cyathea tortuosa* R. C. Moran and small individuals of *C. crenata.* It can be readily distinguished from these two species and any other Neotropical tree fern by the combination of a conspicuous adaxial hirsute indument of intergraded stiff, erect, reddish brown hairs and orange-brown lanceolate squamules, with strongly decurrent fronds (short petioles to 15 cm; basal pinnae ca. 1/5 the length of the medial pinnae, at times so reduced as to resemble a pinnule), and a large number of pinnae (13–15 per frond). Strongly decurrent fronds are known from a few other bipinnate-pinnatifid tree fern species in South America such as *Cyathea acutidens* (H. Christ) Domin and those of the *Cyathea cyatheoides* group (*C. cyatheoides* (Desv.) Kramer, *C. surinamensis* (Miq.) Domin, and *C. bradei* (Windsich) Lellinger). However, all these species, which are not necessarily closely related to *C. cisandina*, lack the conspicuous reddish hirsute indument of the latter.

The closest relatives of *C. cisandina* appear not to be found on the Amazonian side of the Andes but in Central America and along the Pacific coast of South America. The sori, frond disection, and abaxial bullate scales along veins of *C. cisandina* show strong affinities to the *Cyathea brunnescens* group (including *C. brunnescens*, *C. darienensis* R. C. Moran, *C. punctata* R. C. Moran, and *C. wendlandii* (Kuhn) Domin of the Darién-Chocó biogeographic region (Lehnert, 2016). Of all these species, the most similar to *C. cisandina* appears to be *C. wendlandii*, paradoxically the one distributed furthest away,

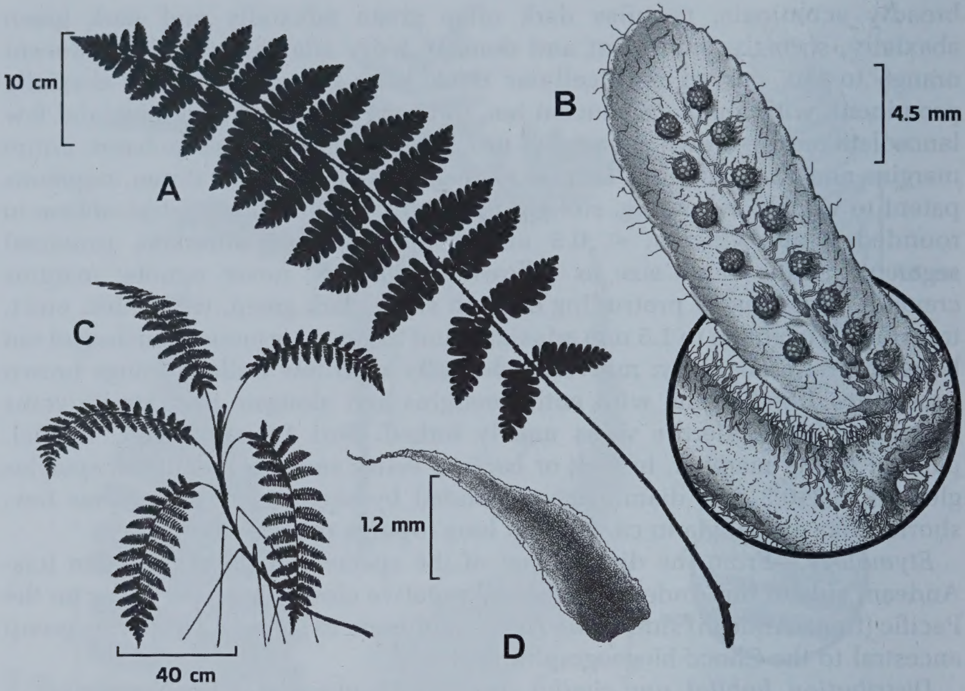

FIG. 4. *Cyathea grata*. **A**. Frond, silhouette. **B**. Fertile segment, abaxially. **C**. Habit. **D**. Petiole scale. (drawn from G. Calatayud 6076 USM, CUZ)

in southern Central America, in which the discordantly bicolorous, matte brown, erose, and slightly indurate petioles scales highly resemble those of *C. cisandina*. In addition to the unique character combination of *C. cisandina*, this species differs from *C. wendlandii* in its wider segments (segment width ca. ½ segment length), narrow, almost ocluded sinuses, and in its shorter, attenuate petiole scale tips. *Cyathea wendlandii*, in contrast, has narrower, longer segments (segment width ca. 1/3 segment length), wide sinuses (ca. 1/3 segment width), and long, caudate petiole scale tips. As it is also the case for *C. wendlandii*, all other species in the *C. brunnescens* group can be distinguished from *C. cisandina* by their lack of a reddish brown hirsute indument on the axes adaxially.

Cyathea grata A. Tejedor and G. Calatayud **sp. nov.** Type: PERU. Cajamarca: San Ignacio, Huarango, trocha de Ozurco a Nuevo Mundo, -5.2417, -78.7208, 1750 m, 11 Oct 2017, *G. Calatayud* 6076 (holotype: USM!; isotypes: CUZ! HOXA!). Fig. 4.

Diagnosis.—Resembling *C. oreopteroides* Lehnert & A. Tejedor but differing in its more slender trunk (to 1.5 cm diam.), long (to 2 mm) tortuous bristles along axes, and its ovate-lanceolate pinnae with crenate margins.

Trunks to 0.5 m tall, extremely slender, 1–1.5 cm diam., decumbent, inermous, retaining old petiole bases, covered in scales similar to those of petioles; apices not hidden, protruding above a loose spiral of remotely set petiole bases; with adventitious buds along trunk length. Fronds to 80 cm long, weakly arching from ascending petioles. Petioles long, to 30 cm long, brittle, sparsely verrucate, epidermis pale olive-brown adaxially, olive-green to reddish brown abaxially, matte, sparsely scurfy, scurf consisting of appressed orange-brown wavy, linear squamules to 1.5 mm long; petioles scaly abaxially extending into rhachises. Petiole scales lanceolate, to 5 × 3 mm, bases truncate, apices attenuate, falcate, flat; discordantly bicolorous with orange brown centers and paler orange-brown, slightly translucent margins; differentiated margins broad, without setae, entire. Laminae to 50 × 17 cm, narrowly lanceolate, pinnate-pinnatifid, firm carthaceous, fragile, shiny dark-green adaxially, paler abaxially; apices gradually reduced. Rhachises sparsely verrucate, abaxially, matte, olive brown adaxially, olive green abaxially; adaxially densely hairy with whitish to translucent, antrorsely appressed, thick multicellular hairs to 1.5 mm long, intergraded with wavy to twisted linear light orange brown squamules to 2.5 mm, abaxially and on the sides with thinner translucent to whitish erect curved hairs to 2 mm long and scales similar to those of petioles but smaller. Pinnae to 7 cm long, short-stalked to 3 mm, ca. 9–10 pairs per frond, patent to weakly ascending, alternate, inarticulate, ovate lanceolate, distal segments weakly decurrently adnate before ending in a pinnatifid apical section; basal pinna pairs slightly shorter than medial pinnae, reflexed. Costae to 2 mm wide, inermous, dark olive green adaxially, paler abaxially, alate along proximal 1/3, epidermis adaxially obscured by dense indument similar to that on rachises, abaxially with golden flat ovate squamules to 2 mm long with caudate twisted tips and smaller golden broadly ovate bullate squamules to 0.2 mm also with caudate twisted tips; insertion of costae and rachises often with denser concentration of twisted linear pale orange brown squamules; junctures weakly swollen abaxially, each bearing a slightly swollen elliptical pneumathode to 1 mm diam., pale brown, with an adjacent dark green spot in fresh specimens. Largest segments 160–180 × 6.0–7.0 mm, segments weakly ascending, oblong, tips obtuse to rounded, sinuses rounded to acute, to 2.0 mm wide; segments alternate, proximal segments smaller than medial segments, proximally remote; margins serrate; veins weakly protruding abaxially, green, with very sparse erect, translucent whitish hairs to 0.5 mm abaxially and denser, similar hairs adaxially; sterile and fertile veins twice to thrice forked; midveins abaxially covered with many translucent erect to tortuous hairs to 1.5 mm long, interspersed with many bullate golden squamules 1.0–0.5 mm, with entire margins and caudate tips; sterile veins simple or forked, fertile veins mostly forked. Sori 1.0 mm diam., submedial, parallel to the margins, in fork of veins; indusia absent, receptacles globose, 0.2–0.3 mm diam., not subtended by squamules, paraphyses few, translucent, much longer than sporangia to ca. 2 mm long. Spores not examined.

Etymology.—The specific epithet, which means "thankful" in Latin, commemorates a ritual of gratitude to the mother of the first author performed near the site where the species was recognized as new.

Addional specimens examined.—PERU. Amazonas: Alto Nieva, trocha a lo largo de cresta de arenisca, -5.6647, -77.7778, 1900 m, 28 Feb 2018, *G. Calatayud* 6238 (CUZ!).

Distribution, habitat, and similar species.—Northern Peru, known from two localities,1750–2600 m, shady understory of stunted forest over sandstone, growing among tree trunks and roots covered in thick mats of bryophytes, to paramo vegetation, among tank bromeliads of the genus *Guzmania.* Judging from the slenderness of its trunk it is possible that *Cyathea grata* might never grow taller than 0.5 m, although in appropriate conditions it might be able to develop a longer, scrambling habit.

Because of its small size, long lanceolate frond, and pinnate pinnatisect lamina, *Cyathea grata* could be confused with many other small tree ferns, including *C. angelica* A. Tejedor & G. Calatayud, *C. bipinnatifida* (Baker) Domin, *C. brucei* Lehnert, *C. leoniae, C.oreopteroides C.palaciosii* R. C. Moran *C peladensis* (Hieron.) Domin and *C.phegopteroides* (Hook.) Domin. These species also have similar habitat and elevation range. Among all these species, *C. grata* stands out because of its thin trunk (to 1.5 cm. diam.), remotely set petiole bases, a highly scaly, protruding trunk apex that is not hidden by a fascicle of petioles, and ovate-lanceolate pinnae. All other species have thicker trunks (2–5 cm diam.), a tightly overlapping petioles that hide the trunk apex, and relatively thinner, lanceolate to linear-oblong pinnae. The characters distinguishing these species from *grata* are summarized in Table 1.

Cyathea novoi A. Tejedor and G. Calatayud, **sp. nov.** Type: PERU. Amazonas: Alto Nieva, cerro de la antena, parches de matorral encima de la antena, -5.6900, -77.7740, 2620 m, 19 Oct 2017, *G. Calatayud 6140* (holotype: USM! isotypes: CUZ! HOXA!). Fig. 5.

Diagnosis.—Resembling *C. valliciergoana* A. Tejedor & G. Calatayud but differing in its erect fronds, oblong-triangular pinnules, tomentose axes abaxially, and moderately thick petiole scurf of appressed cream to tan irregular squamules.

Trunks to 1 m tall, slender, 3–4 cm diam., not spiny, with old petiole bases; apices hidden by fascicles of petioles; without adventitious buds. Fronds to 70 cm long, strongly erect from ascending petioles. Petioles to 25 cm long, sparsely verrucate, scurf moderately thick abaxially, consisting of appressed cream to tan irregularly dissected squamules to 1 mm long; petioles scaly on the sides along the basal third. Petiole scales ovate-lanceolate, to 10 × 4 mm, bases round, apices long acuminate to attenuate, flat to slightly wavy; concolorous, orange brown with paler orange-brown, slightly translucent margins; differentiated margins very narrow, without setae, erose-dentate, fragile, often partially abraded. Laminae to 45 × 20 cm, long elliptic, bipinnate-pinnatisect, chartaceous, fragile, dark matte green adaxially, pale gray-green

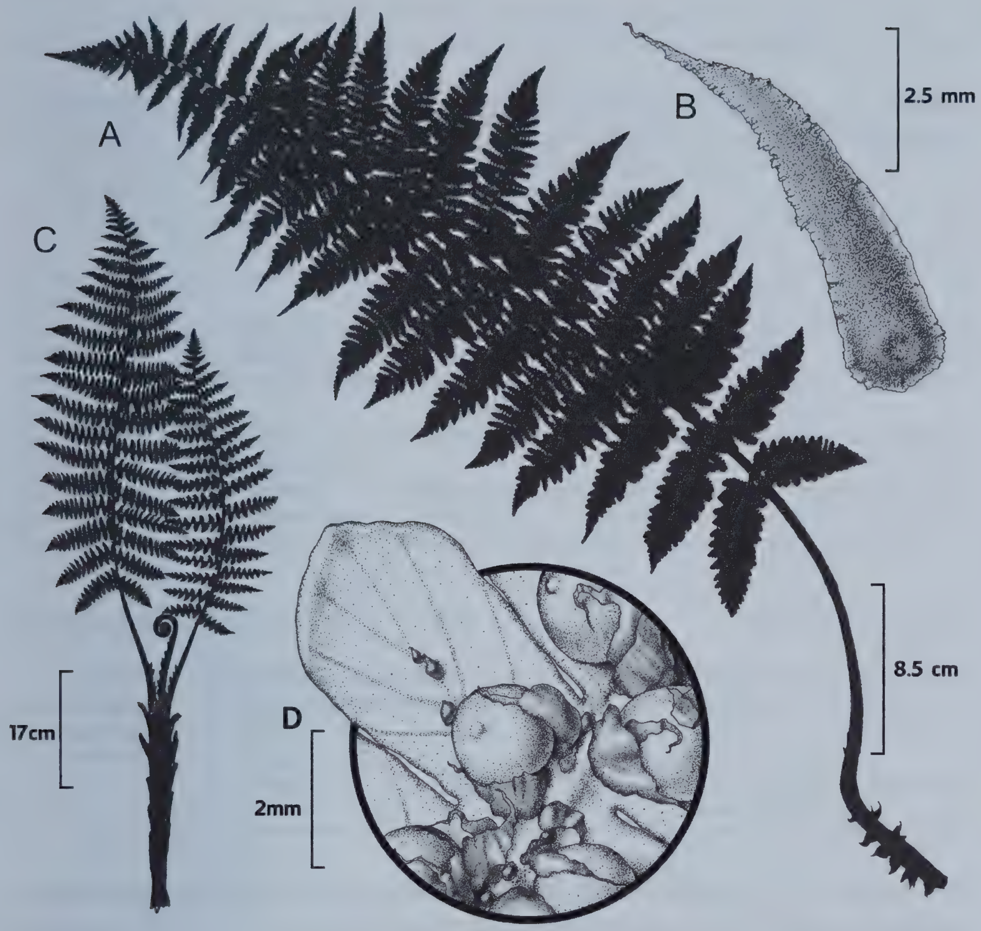

FIG. 5. *Cyathea novoi*. **A**. Frond, silhouette. **B**. Petiole scale. **C**. Habit. **D**. Fertile segment, abaxially. (drawn from G. Calatayud 6140 USM, CUZ).

abaxially; apices gradually reduced. Rhachises inermous, sparsely verrucate abaxially, weakly shiny, olive-green to brownish green abaxially, and dark olive brown adaxially; adaxially densely tomentose with translucent brown, tortuous, matted, multicellular hairs to 1 mm long, abaxially with sparser translucent brown tortuous hairs to 1 mm long interspersed with sub-bullate round brown squamules to 0.3 mm diam. Pinnae to 12 cm long, subsessile to short-stalked to 3 mm, ca. 14 pairs per frond, patent to weakly ascending, alternate to subopposite, inarticulate, narrowly green-alate along distal half, distal pinnules decurrently adnate before ending in a pinnatifid apical section; basal pinna pairs ca. 1/2 the length of the medial pinnae, weakly reflexed. Costae to 3 mm wide, inermous, abaxially verrucate, olive green on both sides, epidermis obscured by dense indument similar to that on rachises; junctures weakly swollen abaxially, each bearing a slightly swollen elliptic

TABLE 1. Comparison of five species of *Cyathea* from northern Peru.

Character	*C. angelica*	*C. bipinnatifida*	*C. brucei*	*C. grata*	*C. leoniae*
trunk apex	hidden by petiole bases	hidden by petiole bases	hidden by petiole bases	**not hidden by petiole bases**	hidden by petiole bases
adventitious buds	absent	occasional	present	present	absent
fronds	erect	patent/arching	drooping	arching	erect
lamina	bipinnate pinnatifid	pinnate pinnatisect	**pinnate**	pinnate pinnatisect	**pinnate pinnatisect**
lamina base	not decurrent	not decurrent	not decurrent	not decurrent	not decurrent
largest pinnules	triangular	linear	lanceolate	**ovate-lanceolate**	linear-lanceolate
petiole bases	persistent	caduceous	persistent	persistent	persistent
rachis	lanuginose on both sides	short pubescent on both sides	short pubescent adaxially	villous on both sides	short pubescent adaxially
petiole scale margins	**fimbriate**	erose	**erose**	erose	entire to erose
petiole scale color	**concolorous stramineous**	brown center light brown margin	**concolorous stramineous**	dark brown center light brown center	nearly concolorous orange brown
indusium	absent **sphaeropteroid**	absent	absent	absent	

pneumathode to 1 mm diam., light green, often with an adjacent conspicuous dark green spot in fresh specimens. Largest pinnules to 15 × 6 mm, pinnules sessile, inarticulate, ca. 6 mm between the stalks/costules, oblong-triangular, bases truncate, equilateral, apices obtuse to rounded; costules dark matte green adaxially, pale gray-green abaxially, planar and inconspicuous adaxially; abaxially slightly raised, with many flat lanceolate orange brown squamules to 2 mm long, with entire margins and long attenuate tips and round to ovate bullate squamules to 0.3 mm. Largest segments 4 × 2 mm, segments patent to weakly ascending, straight, oblong elliptic, tips obtuse to rounded, sinuses acute, occluded; segments sub-opposite to alternate, proximal segments slightly larger than following segments, never remote; margins entire; veins weakly sunken abaxially and planar abaxially, dark green, glabrous; midveins short, quickly branching into veins, infrequently with few round to ovate bullate orange brown squamules to 0.3 mm abaxially. Sori 1.0 mm diam., usually one, rarely two per segment, adjacent to costule, in fork of midveins; indusia sphaeropteroid, with prominent umbo, receptacles and paraphyses not observed. Spores not examined.

TABLE 1. Extended.

C. oreopteroides	*C. palaciosii*	*C. peladensis*	*C. phegopteroides*	*C. novoi*
hidden by petiole bases	hidden by petiole bases	hidden by petiole bases	hidden by petiole bases	hidden by petiole bases
present	present	present	Absent	absent
ascending to spreading	spreading	arching	patent/arching	erect
pinnate pinnatisect	pinnate pinnatisect	pinnate pinnatisect	pinnate pinnatisect	**bippinnate pinnatisect**
not decurrent	not decurrent	not decurrent	**strongly decurrent**	not decurrent
linear-lanceolate	linear-lanceolate	linear	linear	ovate lanceolate
persistent	persistent	caduceous	caduceous	persistent
adaxially and abaxially	**pilose on both sides**	short pubescent on both sides	pubescent on both sides	tomentous on both sides
entire to erose	entire to erose	erose	erose	erose
dark brown center light brown margin	**light brown centers tan margin**	**dark brown center stramineous margin**	brown center light brown margin	nearly concolorous orange brown
absent	absent	**hemitelioid**	absent	sphaeropteroid

Etymology.—The specific epithet honors Roberto (Chachi) Novo, honorary uncle of the first author, whose photographic memory of landscapes led to productive field sites.

Distribution, habitat, and similar species.—Northern Peru, known only from type locality on a sandstone mountain, patches of perhumid low scrub within páramo-like vegetation dominated by tank bromeliads of the genus *Guzmania*. Its erect, nearly vertical fronds rise above the surrounding vegetation.

Several other small tree ferns share this habitat with *C. novoi*, including *C. grata*, *C. leoniae*, *C. microphylla* Mett. *C. pibyae* A. Tejedor & G. Calatayud plus small individuals of *C. meridensis var. obtecta* Lehnert and *C. praetermissa* Lehnert, both of which attain large sizes and develop tall trunks in areas with deeper soils and denser forest.

In the field, the erect fronds with patent pinnae of *Cyathea novoi* readily set it apart from most of the species mentioned above, all of which, except *C. leoniae*, have arching to drooping fronds and pinnae. *Cyathea leoniae*, on the other hand, has a size and habit highly reminiscent of those of *C. novoi*. The two species, nonetheless, are easily distinguished by lamina division and indument. *Cyathea novoi* has bipinnate-pinnatisect laminae, a tomentose rachis on both sides, moderately thick scurf on the petiole abaxially consisting of appressed cream to tan irregularly dissected squamules to 1 mm long, and petiole scales with markedly erose to dentate margins. *Cyathea leoniae*, in contrast, has pinnate-pinnatisect laminae, a rachis pubescent only adaxially being glabrous or glabrescent abaxially, pulverulent scurf consisting of concolorous, castaneous to brown, irregularly shaped to ovate-lanceolate squamules 0.3–0.8 mm, and petiole scales with entire to slightly erose margins.

In the herbarium, where field characters such as frond orientation are harder to ascertain, *C. novoi* may be most easily confused with *C. valliciergoana* and *C. microphylla*. From *C. valliciergoana*, *C. novoi* differs in its oblong-triangular pinnules, tomentose rachis abaxially, and the moderately thick cream to tan scurf. *Cyathea valliciergoana*, in contrast, has oblong pinnules, glabrous rachis abaxially, and thin ephemeral scurf of golden brown arachnoid squamules. From *C. microphylla*, *C. novoi* differs in its lanceolate, concolorous orange brown petiole scales, oblong-triangular pinnules, and oblong-elliptic, adnate segments, with entire margins. *Cyathea microphylla*, in contrast, has broadly ovate, bicolorous petiole scales, with central brown spot and stramineous margins, oblong pinnules, and obovate segments, free along the basal half of the pinnule, with lobate margins.

The long elliptic, erect fronds of *Cyathea novoi*, make this species vaguely similar in the field with several small to dwarf tree ferns such as *C. angelica*, *C. bipinnatifida*, *C. oreopteroides*, *C. palaciosii*, *C peladensis*, and *C. phegopteroides*. *Cyathea novoi* can be distinguished from those species by the characters listed in Table 1.

Cyathea oscarorum A. Tejedor & G. Calatayud, **sp. nov.** Type: PERU. Cajamarca: San Ignacio, El Porvenir, La Montaña Negra, arenal frente a finca de la familia Díaz Pérez -5.1380, -78.7487, 1816 m, 7 mar 2018, *G. Calatayud* 6300 (holotype: USM!; isotypes: CUZ! HOXA!). Figs. 2, 6.

Diagnosis.—Resembling *Cyathea gracilis* but differing in its ascending fronds that arch only at the tips, horizontal pinnae and pinnules, moderately thick scurf of hairs and squamules, acute pinnule tips, and conspicuous tufts of scales at the insertions of pinnae with rachis and pinnules with costae.

Trunks erect to decumbent, to 2 m tall, thick, to 9–11 cm diam., thickly covered with old petiole bases; trunk apex hidden between petiole bases, these often bent irregularly forming an untidy fascicle. Fronds to 2 m long, first ascending then arching at the tips, forming a fountain-like crown. Petioles to 60 cm long, sparsely verrucate, dark olive green adaxially and matte brown abaxially, with moderately dense scurf consisting of matted tortuous hairs to 1 mm long interspersed with reddish brown lanceolate squamules to 1 mm long; petioles on each side with a discontinuous line of orange-brown lenticels to 10.0–15.0 × 1.0–2.0 mm, scaly along basal half, scales caducous and retained only at base in older petioles. Petiole scales lanceolate, 20.0–25.0 × 3.0–4.0 mm, matte, bicolorous reddish brown with very narrow light brown margins, apices attenuate, wavy to twisted; differentiated margins fragile, often abraded. Laminae to 140 × 90 cm, ovate triangular, bipinnate-pinnatisect to proximally

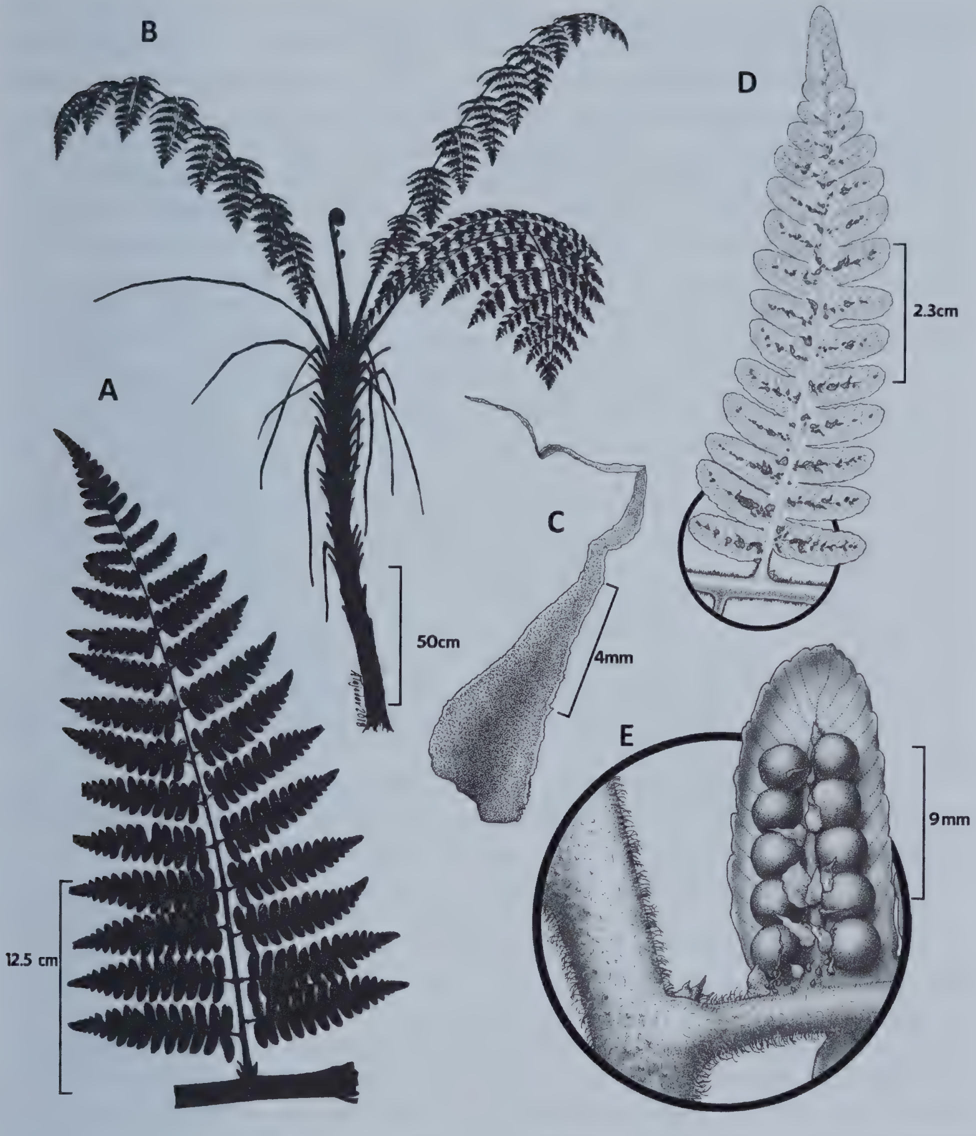

FIG. 6. *Cyathea oscarorum.* **A.** Pinna, silhouette. **B.** Habit. **C.** Petiole scale. **D.** Infertile pinna abaxially. **E.** Fertile segment abaxially. (drawn from G. Calatayud 6300 USM, CUZ).

tripinnate, subcoriaceous, matte, dark to dull green adaxially, paler abaxially; 9–10 pinna pairs, basal ones not to only slightly reflexed about the same length of medial pinnae; apices gradually reduced. Frond axes verrucate, dark olive green to olive brown, dull brown abaxially, matte, adaxially with thin scurf of pale tortuous hairs to 1.0 mm long interspersed with linear to lanceolate reddish brown squamules, contrasting with dark green epidermis, easily abraded leaving scabrous surface, abaxially with similar but denser indument, pale hairs more strongly contrasting with brown epidermis; costae to 6.0 mm wide, junctures of costae and rachises swollen, abaxially with two large, conspicuous, protruding elliptic aerophore to 6.0 × 2.5 mm, yellowish green. Pinnae to 50 cm long, patent, long stalked to 4.5 cm, alternate, articulate, distally weakly green-alate, ending in a pinnatifid apical section. Pinnules to 9 × 3 cm, long stalked to 14 mm, articulate, 1.5–2 cm between the stalks, triangular, tips acuminate, costules olive brown adaxially, carnose abaxially, abaxially strongly prominent, with tortuous whitish hairs to 1 mm long interspersed with bullate and flat lanceolate squamules to 1.0 mm, reddish to orange brown. Segments to 18 × 5 mm, sessile, usually adnate but occasionally remote, slightly ascending, oblong, tips obtuse to rounded, alternate, proximal segments usually longer than following segments, basal segments strongly asymmetric; sinuses oblong to acute to 4.0 mm wide; margins crenulate; midveins protruding abaxially, green, with very sparse hairs to 1 mm long; veins flat, ending at the margins, glabrous on both sides; with flat, reddish to orange brown lanceolate squamules to 1.0 mm, and orange-brown bullate squamules to 0.5 mm long; sterile and fertile veins usually forked, more rarely simple. Sori 1.0–1.2 mm diam., subcostal, more or less parallel to midvein, in the fork of veins; indusia sphaeropteroid with prominent umbo, opaque, rich reddish brown; paraphyses shorter than sporangia. Spores not examined.

Etymology.—The specific epithet honors Oscar Tejedor Jr. and Oscar Tejedor Sr., father and grandfather of the first author, who taught him to look at nature with awe and skepticism.

Distribution, habitat, and similar species.—Northern Peru, frequent in scrub, pastures, and open, low woodland on relatively dry, well-drained facies of sandstone ridges, often under full sun,1700–2600 m.

It co-occurs with several other tree ferns including *Cyathea chontilla* Lehnert, *C. divergens* Kunze *C. gracilis* Griseb. *C. thelypteroides* A. R. Smith, *C. villosa* Humb. & Bonpl. ex Willd. and *C. lindeniana*, although the latter rarely grows outside of the shade of tree islands or forest. In its open habitat, *Cyathea oscarorum* is generally the tallest, most conspicuous tree fern, with its ascending fronds, and often also its trunk, growing well above the surrounding shrubs and herbaceous vegetation. At the margins of its distribution it can also co-occur with *C. pibyae* (at transitions to wetter areas) and with *C. xerica* (at the transition to higher elevations).

In the field, *Cyathea oscarorum* is most similar to *C. gracilis* in size and general aspect of the habit and particularly in the thick fascicle of old petiole bases around the trunk apex. It can be distinguished from *C. gracilis* by its ascending fronds that usually arch only at the tips, triangular, horizontally held pinnae and pinnules, shorter, acute pinnule tips, matte and usually darker green lamina, moderately thick scurf of hairs and squamules, which imparts a slightly fuzzy texture to frond axes both adaxially and abaxially, lanceolate, less caducous, dull brown petiole scales that are only slightly bicolorous, and especially by the conspicuous tufts of scales at the insertions of pinnae with rachis and pinnules with costae. *Cyathea gracilis*, in contrast, has markedly arched fronds that droop at least for most of their distal third, lanceolate, drooping pinnae and pinnules, long attenuate pinnule tips, a shiny and usually brighter green lamina, no scurf to quickly caducous scurf along axes, which are therefore usually shiny on both sides, ovate, lustrous, bicolorous brown scales with broad lighter brown margins, and no tufts of scales at insertions of pinnae to rachis and pinnules with costae.

Cyathea chontilla is another species similar to *C. oscarorum* and that also co-occurs with it. The two species are readily distinguished in the field because *C. oscarorum* has mostly ascending fronds that arch downward at the tips, horizontally held pinnae and pinnules, usually alternate pinnae, and less well developed indument, with petiole scales mostly confined to petiole bases, sparser scurf, and conspicuous tufts of scales at insertions of pinnae to rachis and pinnules with costae. *Cyathea chontilla*, on the other hand, has entirely upright fronds that arch upwards from the petiole base, ascending, revolute pinnae and pinnules, subopposite pinnae, a thick indument of petiole scales plus dense scurf of hairs and squamules along all frond axes, and a usually smaller overall size. These distinguishing characters, with the exception of overall size, are also reliable to distinguish juveniles of the two species, with young plants of *C. chontilla* showing upright fronds and revolute pinnae whereas those of *C. oscarorum* show horizontal or flat fronds and pinnae. In the herbarium, on the other hand, where characters concerning habit and position of fronds are lost, distinguishing material of these two species may be more difficult and badly preserved specimens of *C. chontilla* that lack petioles and have abraded indument might be easily mistaken for *C. oscarorum*. In this context, the difference in pinnule shape between these species should help distinguish the two. *Cyathea chontilla* has short-stalked, more oblong pinnules with obtuse to rounded apices whereas *C. oscarorum* has petiolulate, triangular pinnules with acute to acuminate apices.

Cyathea pibyae is also a similar species that occasionally co-occurs with *C. oscarorum* but the two species are usually separated along humidity and elevation gradients, with *C. pibyae* occurring at higher elevations and in wetter environments such as the windward side of ridges facing incoming clouds or within thicker, mossier scrub. *Cyathea oscarorum* differs from *C. pibyae* in its larger size (fronds to 2 m), and has thicker trunks to 11 cm diam., a denser, thicker fascicle of old petiole bases around the trunk apex, less dissected fronds with relatively shorter pinnae stalks and basal segments of pinnules usually adnate, rarely remote, more ovate fronds with basal pinnae about as long as medial pinnae, usually alternate pinnae, and ascending fronds, only arching downward at tips, with horizontally held pinnae and pinnules. *Cyathea pibyae*, in contrast, is smaller (fronds usually $<$ 1 m long, rarely to 1.3 m), slender trunks to 5 cm diam., thinner, cleaner trunk apex with three to four old petiole bases, more dissected frond with relatively longer pinnae stalks and basal pinnule segments usually remote, more triangular fronds with the largest pinnae at the base, usually subopposite pinnae, and more strongly arching to drooping fronds with usually drooping pinnules.

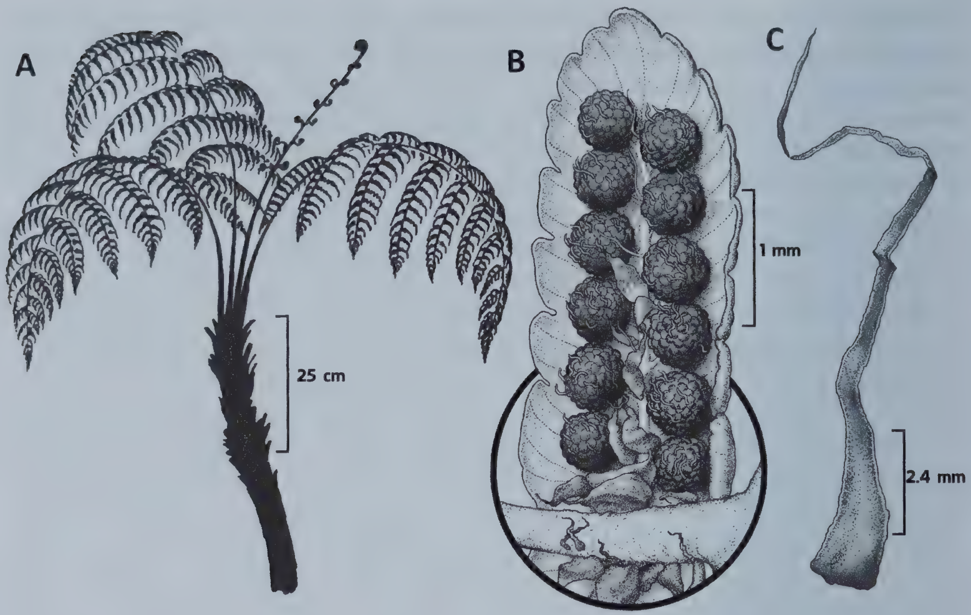

Fig. 7. *Cyathea phoenix*. **A**. Habit, silhouette. **B**. Fertile segment, abaxially. **C**. Petiole scale. (drawn from G. Calatayud 6140 USM, CUZ).

Cyathea phoenix A. Tejedor & G. Calatayud, **sp. nov.** Type: PERU. Amazonas: Bagua, La Peca, trocha a la cima de la pared de arenisca al norte de La Peca, -5.5724, -78.4185, 1825 m, 27 Oct 2017, *G. Calatayud 6163* (holotype: USM!; isotypes: CUZ! HOXA!). Fig. 7.

Diagnosis.—Resembling a small *C. lindeniana* but differing in its lack of indusium and sparsely hairy axes abaxially.

Trunks to 70 cm tall and 7 cm diam., not spiny, retaining old petiole bases; apices hidden by fascicles of petioles; without adventitious buds. Fronds to 1 m long, strongly arching from ascending petioles. Petioles long, to 40 cm long, verrucate, epidermis dark olive-green when young to reddish brown and atropurpureous at different stages of frond maturity, dark brown when dried, scurf thin and caducous, consisting of sparse appressed linear brown squamules to 0.5 mm long interspersed with appressed, thin, translucent hairs to 0.5 mm long; petioles scaly both adaxially and abaxially along the basal half, but petiole scales caducous and retained only at petiole base in older fronds. Petiole scales linear-lanceolate, to 19 × 2 mm, bases round to truncate, apices long attenuate, twisted; concolorous to slightly bicolorous orange-brown with paler orange-brown margins hardly contrasting with a central darker brown streak of variable width; differentiated margins entire along distal half, margins arose and whitish along basal half. Laminae to 60 × 40 cm, ovate, bipinnate-pinnatisect, chartaceous, bright olive-green adaxially, paler abaxially; apices gradually reduced. Rhachises inermous, matte dark olive-green adaxially, weakly shiny yellowish green to brownish green abaxially; adaxially densely sericeous with translucent brown, tortuous, matted, multicellular hairs to 1 mm long, abaxially with sparser appressed translucent whitish tortuous hairs to 10 mm long interspersed with appressed linear brown squamules to 1.5 mm long. Pinnae to 26 × 12 cm, stalked to 1 cm, 6–8 pairs per frond, oblong-lanceolate with narrowly acute apices, patent to weakly ascending, alternate to opposite, inarticulate, non-alate, distal pinnules decurrently adnate before ending in a pinnatifid apical section; basal pinna slightly shorter than longest pinnae, not reflexed. Costae to 2 mm wide, inermous, matte olive green adaxially, shiny yellowish green to carnose abaxially, adaxial epidermis obscured by indument similar to that on rachises; junctures adaxially bearing tufts of linear-lanceolate brown scales to 1.5 cm long, abaxially not swollen, bearing a slightly swollen elliptic pneumathode to 0.3 mm diam., yellowish green. Largest pinnules to 5 × 1 cm, pinnules sessile to short stalked to 1 mm, inarticulate, ca. 13 mm between the stalks/costules, lanceolate, bases truncate to slightly oblique, equilateral, apices long acute; costules olive green adaxially, pale yellowish green to carnose abaxially, conspicuously raised on both sides, bearing a few scattered translucent, appressed wavy hairs ca. 1 mm long or glabrescent, with a few flat ovate to lanceolate orange brown squamules to 1 mm long, with entire margins and long attenuate tips. Largest segments 4 × 2 mm, segments patent to weakly ascending, straight, oblong elliptic, tips obtuse to rounded, sinuses acute to 0.3 mm wide; segments sub-opposite to alternate, proximal segments slightly larger than following segments, never remote; margins crenulate; veins weakly sunken abaxially and weakly raised abaxially, green, adaxially with hairs similar to those of rachises, abaxially glabrous; midveins with many flat ovate to lanceolate orange brown squamules to 1.5 mm long, with entire margins and long attenuate tips. Sori 1.0 mm diam., medial, in fork of veins; indusia absent, paraphyses few, hyaline, slightly longer than sporangia, receptacles globose, to 0.4 mm diam. Spores not examined.

Etymology.—The specific epithet refers to the mythological bird that resurrects from its own ashes, in reference to the species' ability to resprout after its green parts are burnt down by fire.

Distribution, habitat, and similar species.—Northern Peru, known only from type locality, lower montane grassland and open scrub on white sandstone.

Cyathea phoenix co-occurs with four other tree fern species (*C. aterrima*, *C. chontilla*, *C. gracilis*, and *C. oscarorum*), and, like them, resprouts after being burnt by fire. At the time of collection, the type locality was recovering from a fire that had taken place less than a year before and while most shrubs and treelets had been partially burnt or completely killed, *C. phoenix* and the other three species with which it coexists were rebounding with full crowns of fresh fronds above charred short trunks. *Cyathea lindeniana*, the species that *C. phoenix* resembles the most in lamina division and general aspect, grows in the vicinity of *C. phoenix* but rarely outside of forest patches and seems much less resistant to fire, with most plants observed showing the growing apex severely burnt and desiccated and looking apparently dead.

Cyathea phoenix can be distinguished from among its sympatric species by the combination of exindusiate sori, concolorous orange brown scales, and glabrescent axes with sparse appressed tortuous hairs that when lost leave a slightly scabrous surface. Most of the potentially confusable species, *C. chontilla*, *C. gracilis*, *C. lindeniana*, and *C. oscarorum* have a sphaeropteroid indusium, the exception being the exindusiate *C. aterrima*, which differs from *C. phoenix* by its densely villose axes. Young individuals of *C. delgadii,* so far not found at the type locality of *C. phoenix*, could be confused with *C. phoenix* but it also has a sphaeropteroid indusium and a short pubescent lamina adaxially, whereas the lamina of *C. phoenix* is glabrous, only rarely showing one or two tortuous bristle along a main vein. Finally, *C. phoenix* could be confused with small individuals of the exindusiate *C. poeppigii*, but these always have petiole scales that are nearly concolorous stramineous or bicolorous with brown centers and stramineous margins.

Discussion

The new species described here increase the tree fern species richness of Peru to 108 species and the relative contribution of the Amotape-Huancabamba Zone (Weigend, 2002; 2004; from here on the AHZ) to the Peruvian tree fern flora. These results emphasize the strong latitudinal gradient of species richness of tree ferns in the central Andes (Tejedor, 2017). Equatorial, less seasonal northern Peru (including the departments of Cajamarca, Amazonas, and San Martin) now is known to harbor 92 species of tree ferns, twice as many as the number of tree ferns known from southern Peru (including the departments of Puno and Cusco), and appears to be a center of diversity of Cyatheaceae in the Neotropics. The new taxa described here, confirm predictions that additional species of tree ferns should be found in the highly dissected geomorphologic mosaic of the AHZ, and that many of these species would be small tree ferns from sandstone substrates (Lehnert and Tejedor, 2016; Tejedor and Calatayud, 2017).

All the species described here were found on soils developed directly on sandstone bedrock or scree, spanning habitats from the wetter, windward (eastern or northeastern) side of mountain ranges to drier scrub on the leeward (western or southwestern) side, passing through stunted scrub or páramo on cloud-swept ridges and perhumid rock faces. *Cyathea cisandina* was found under tall forest on sandstone scree in the wettest side of the gradient, whereas *C. oscarorum* and *C. phoenix* were found on the drier scrub of leeward slopes growing under full sun. Among the species described here there does not seem to be a clear relationship between apparent water availability and body size because the two tallest species, *C. cisandina* and *C. oscarorum*, occurred on opposite ends of the humidity spectrum. Two small species from open habitats, *C. phoenix* and *C. novoi*, on the other hand, do show two syndromes hypothesized to be strategies to minimize insolation during cloudless days (Tejedor and Calatayud, 2017). Namely, *C. phoenix* showed markedly arching fronds and drooping pinnules, whereas *C. novoi* showed strongly erect fronds and vertically aligned pinnae, two apparently opposite strategies that may expose minimum leaf surface to the midday sun. One species, the slender, decumbent *C. grata*, appeared to be the most ecologically eclectic, occurring on wet sandstone ridges, in páramo vegetation, and in dry leeward slopes, but always in relatively protected settings, either among well-shaded mossy tree roots, or in cavities formed among clumps of tank bromeliads.

With the exceptions of *C. cisandina,* with putative closest congeners on the Costa Rica-Chocó biogeographic region (as defined by Barthlott et al., 2005) and *C. carolinae*, which seems to belong among species of the Andean indusiate clade (the *C. divergens* clade of Korall et al., 2007), the remaining four species described here appear to have affinities with the sandstone-associated alliances that straddle the Andes and the Guiana Highlands including those of the *Cyathea lechleri/C gracilis* group (represented here by *C. oscarorum,* and *C. novoi*), the *C. aterrima* group (*C. phoenix),* and the *C. bipinnatifida* group (*C. grata*). This small group of newly described species, thus, exemplify the mixed biogeographic nature of the AHZ, which seems to be a biological crossroads between three centers of global plant diversity, the Andes-Amazonia Center, the Costa Rica-Chocó Center, and the Guayana Center (Barthlott et al., 2005; Knapp, 2002; Knapp, 2010; Neill, 2005). Whether most of the sandstone-associated species of the AHZ are narrow endemics restricted to one or a few isolated outcrops or have wider distributions within or even outside the AHZ remains to be discovered with future fieldwork.

Acknowledgments

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A New Species, New Combinations in *Pecluma* and *Pleopeltis*, and New Records for the State of Veracruz, Mexico

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Abstract.—We describe ***Pleopeltis constricta*** Sprunt & Hickey as a new species from El Salvador and Mexico and additionally provide eight new fern records for the State of Veracruz. Furthermore, we propose one new combination each in *Pecluma* (***P. liebmannii*** (C. Chr.) A. R. Sm. & Carv.-Hern.) and *Pleopeltis* (***P. acicularis*** (Weath.) A. R. Sm. & T. Krömer). These novelties bring the new total for Veracruz to 574 species.

Key Words.—*Asplenium*; *Elaphoglossum*; ferns; humid montane forest; *Polypodium*; tropical lowland rainforest.

Mexico, with more than 1000 recorded species, has one of the best-documented fern floras in the world (Mickel and Smith, 2004). However, within the last decade several species found within the country were described as new to science (e.g., Hirai, Sundue, and Prado, 2014; Krömer, Acebey, and Smith, 2007; Li, Pryer, and Windham, 2012; Moran and Prado, 2010; Sigel *et al.*, 2014, Sundue, 2017) and dozens of new state records have been discovered, especially for Oaxaca (Hernández-Rojas *et al.*, 2018), Tabasco (Carvajal-Hernández *et al.*, 2018), and Veracruz (Krömer *et al.*, 2015).

The state of Veracruz harbors 564 fern and lycophyte species and is one of three Mexican states, together with Chiapas (697 species) and Oaxaca (667), with the highest number of species (Krömer *et al.,* 2015; Mickel and Smith, 2004). Within Veracruz, the richest area is in the Los Tuxtlas Biosphere Reserve, where 246 taxa have been recorded (Acebey *et al.*, 2015), and within the central mountains, where 197 taxa have been found (Carvajal-Hernández, Krömer, and Vázquez-Torres, 2014; Carvajal-Hernández and Krömer, 2015).

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* corresponding author

Generally, the humid montane forests of Veracruz contain the most species – about 66% of all ferns of the state occur in this vegetation type (Tejero-Díez *et al.*, 2011). However, tropical lowland rain forests are also rich in ferns; e.g., Acebey *et al.* (2015) recorded about 115 species (vs. 134 in humid montane forests) for Los Tuxtlas in this ecosystem.

Unfortunately, these two vegetation types have very high deforestation rates and are seriously threatened by land-use changes in Veracruz (Ellis, Martínez-Bello, and Monroy-Ibarra, 2011); this endangers the pteridophyte flora of these areas, especially of epiphytic groups, such as grammitids and the lycophyte genus *Phlegmariurus* (Armenta-Montero *et al.*, 2015; Krömer, Acebey, and Smith, 2013). Consequently, species richness of ferns in central Veracruz has been significantly reduced by 37–63% in disturbed and secondary forests compared to natural forests (Carvajal-Hernández *et al.*, 2017). This highlights the need for additional field work in the remaining old-growth forest fragments of remote and botanically largely unexplored areas (Prance *et al.*, 2000), and there are still many parts of the state that lack a good floristic inventory (Gómez-Pompa, Krömer, and Castro-Cortés, 2010). In addition, a thorough review of fern collections in national and local herbaria may reveal range extensions or even species new to science (Bebber *et al.*, 2010; Krömer *et al.*, 2015).

Existing evidence from both morphology and molecular data suggests that some fern genera are not monophyletic. Sometimes, the evidence for polyphyly has come through examination of morphological characters (e.g., Tejero-Díez *et al.*, 2010) or other evidence derived from molecular studies (e.g., Schneider *et al.*, 2004). One of the most problematic genera is *Polypodium s.l.* (Polypodiaceae), of which many genera have been segregated in the last two hundred years, including *Pecluma* and *Pleopeltis.* In the last two decades, several relevant studies have placed former *Polypodium* species into these genera by the publication of new combinations (Assis *et al.*, 2016; Otto *et al.*, 2009; Salino, 1998, 2009; Smith and Tejero-Díez, 2014; Sprunt *et al.*, 2011). In Mexico there are still several species recognized as *Polypodium* that probably belong to other genera (Mickel and Smith, 2004).

MATERIALS AND METHODS

In the course of studies on the diversity and distribution of ferns and vascular epiphytes, we conducted extensive fieldwork between 2015 and 2017, mainly in the central montane region of Veracruz and the southern tropical lowland area of Uxpanapa. We also reviewed herbarium specimens of ferns from Veracruz deposited in the herbarium of the Instituto de Investigaciones Biológicas, Universidad Veracruzana, Xalapa (CIB), National Herbarium of Mexico, Universidad Nacional Autónoma de México, Mexico City (MEXU), and the University Herbarium, University of California, Berkeley (UC). At UC we found the designated "holotype" of *Pleopeltis constricta* Sprunt & Hickey (Sprunt, 2010), a name that has heretofore not been validly published. In agreement with Susan Sprunt, we have decided to include this new species in the present study. Sprunt has kindly sent us descriptive information and photographs of specimens seen by her from F, MICH, NY, and US, and we augment this with some additional observations; however, we credit Sprunt and Hickey for the publication of the new species.

The list below of new fern records for Veracruz generally follows the taxonomy adopted by Mickel and Smith (2004); however, we propose new combinations for two species previously recognized as *Polypodium*. We also provide information about the municipality where collected (available vouchers are cited), as well as data on life form, vegetation type, and elevational range for species in Veracruz. Global and Mexican state distribution data for each species can be found in Mickel and Smith (2004), but we still mention if a taxon was recorded afterwards for a specific state.

RESULTS

Our revision reveals nine species in nine genera as new records for the state of Veracruz, including *Pleopeltis constricta*, a new species to science (Figs. 1–3). Additionally, we give new combinations in *Pecluma* and *Pleopeltis* for two species previously placed in *Polypodium*.

1. ***Pleopeltis constricta*** Sprunt & Hickey, **sp. nov.** TYPE: MEXICO. Oaxaca: Distrito Ixtlán, 15 km S of bridge at Valle Nacional, trail from Puerto Eligio east toward Soyalapam, 2400–1500 ft [700–450 m], 17 Sep 1972, *J. T. Mickel & L. Pardue 6533* (holotype: UC!) (Fig. 1 A).

Differing from all other species of the *Pleopeltis polypodioides* (L.) Watt complex by the contracted pinna bases, at least in the lower part of the blades; this feature renders the blades fully pinnate (Fig. 1 B). In some specimens the proximal pinnae are even short-stalked to ca. 0.5 mm. In older, more mature fronds, this constricted attachment is often associated with a dark, often shiny costa base. *Pleopeltis constricta* differs from *P. acicularis* (Weath.) A. R. Sm. & T. Krömer also by the smaller size of its abaxial rachis scales and the lower density of abaxial laminar scales.

Rhizomes 1.6–1.8 (1.76) mm diam.; rhizome scales imbricate, lanceolate, 0.7–2.3 (1.5) mm long, 0.25–0.5 (0.34) mm wide, bicolorous, central band black, sclerotic, 0.3–1.20 (0.6) mm long, borders narrow, pale-brown to hyaline, margins strongly serrate; leaves monomorphic; stipes 22–73 (51) mm long, covered with lanceolate scales; laminae deeply pinnatisect or narrowly adnate distally, fully pinnate proximally, with 8–13 pinna pairs, pinnae linear-lanceolate to narrowly-elliptic, 43–89 (64) mm long, 16–30 (23) mm wide, the pinnae constricted and sessile or even short-stalked to 0.5 mm; glands inconspicuous, borne on acroscopic side of the proximal pinnae; venation obscure, veins once-forked; adaxial laminar scales scattered, subulate, 0.17–0.58 (0.37) mm long, 0.08–0.23 (0.12) mm wide, golden red, bases pectinate-stellate, apices long-caudate, margins weakly erose; abaxial laminar scales imbricate, lanceolate, mostly touching, with some lamina visible, 0.24–0.81 (0.5) mm long, 0.13–0.24 (0.18) mm wide, bases round, margins undulate, weakly erose, each with a central dark tan to brown band extending into a caudate apex, borders

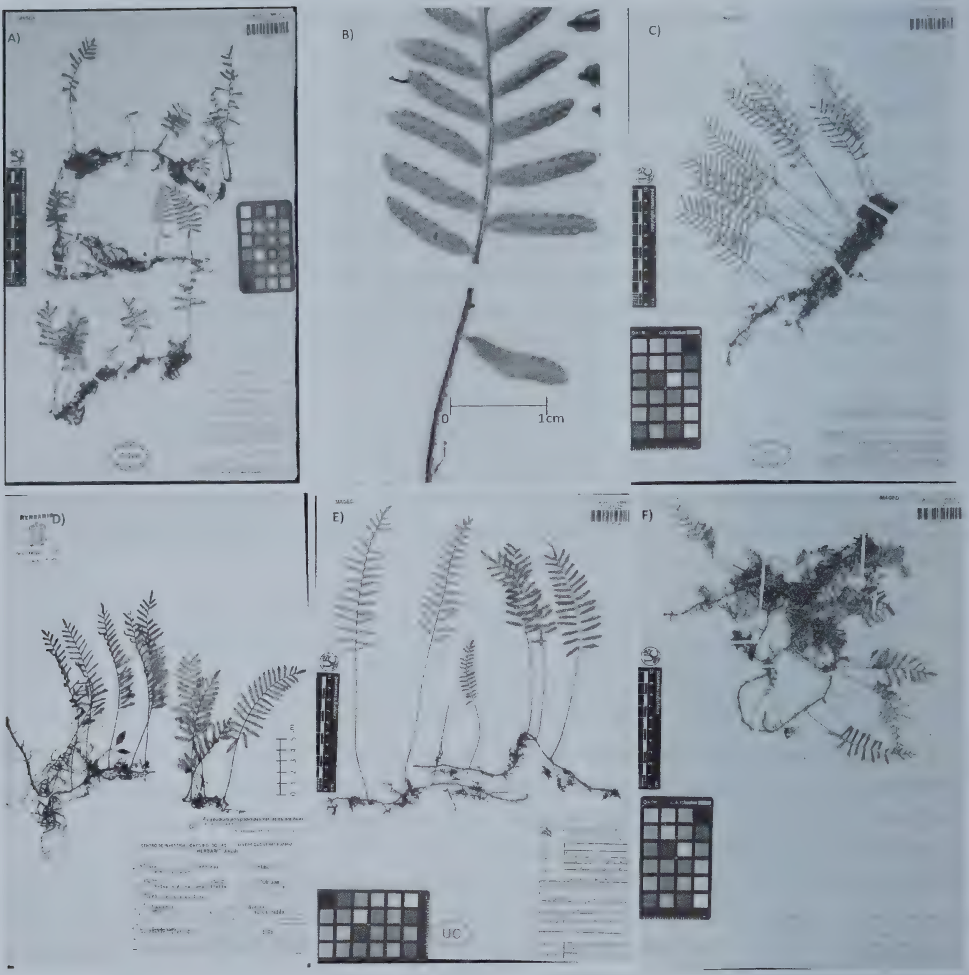

FIG. 1. Images of *Pleopeltis constricta* Sprunt & Hickey A) Holotype *J. T. Mickel & L. Pardue 6533* (UC); B) detail of holotype showing the most distinctive features, which are the contracted pinna bases, at least in the lower part of the blades; C) Paratype *B. T. Gittins 4138* (UC); D) Paratype *R. Acosta et al. 1521* (CIB); E) Paratype *T. Krömer et al. 2703* (UC); F) Paratype *C. A. Purpus 15736* (UC) (Photographs A, B, C, E, F by The University & Jepson Herbaria, University of California, Berkeley; and D by C. I. Carvajal-Hernández).

pale tan, orbicular scales also present; abaxial rachis scales imbricate, lanceolate, usually attached at a 45° angle along rachises, 0.5–1.1 (0.74) mm long, 0.16–0.34 (0.24) mm wide, bicolorous, bases round, apices cuneate, margins weakly erose; sori round to elliptic, uninerved, generally confined to distal half of leaf blade; spores 40–42 (41) μm long, 29–31 (30) μm diameter.

ADDITIONAL SPECIMENS EXAMINED.—El Salvador. Volcán de San Salvador, trail from San Ramón to summit of El Picacho, 1700 m, 15 Jan 1978, *R. Seiler 215* (F, image seen). Mexico. Chiapas: Mpio. Ocosingo, 6-8 km North of Ocosingo

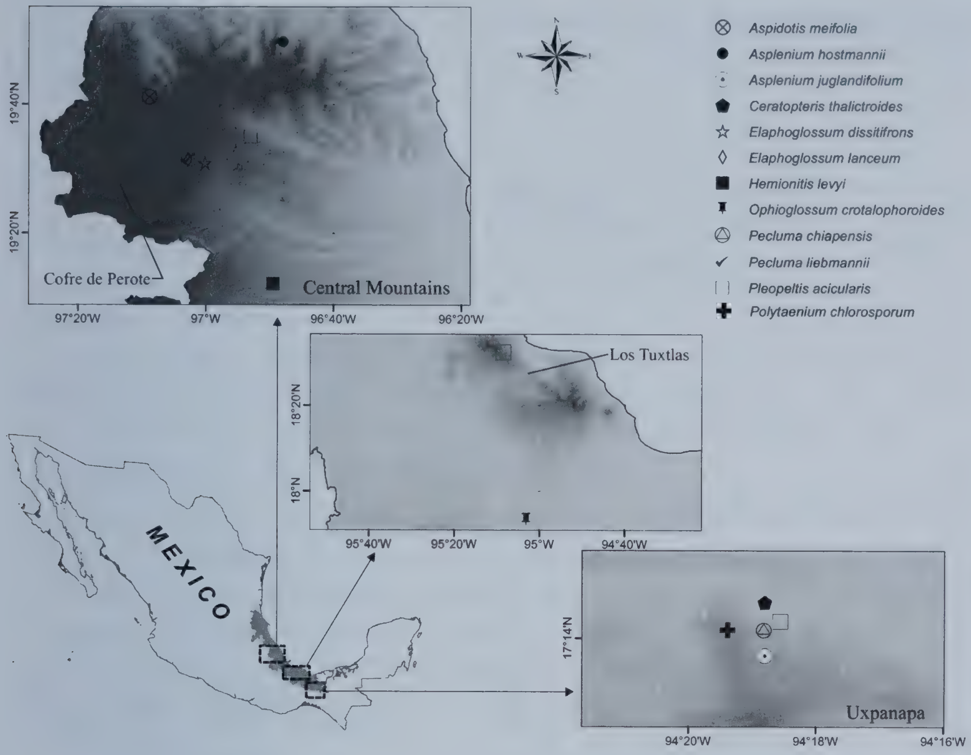

FIG. 2. Distribution map of the new pteridophyte records and new combinations for the State of Veracruz, Mexico.

along road to Bachajon, 900 m, 9 Nov 1971, *D. E. Breedlove & A. R. Smith 22122* (F, image seen); Linda Vista Tropical Biology Station, Pueblo Nuevo Solistahuacan, 5200 ft [1585 m], 22 Aug 1967, *B. T. Gittins 4138* (UC!) (Fig. 1 C). Oaxaca: Mpio. San José de Tenango, Sierra Mazateca, 1420 m, 28 Feb 1992, *G. Ingela 95-M131* (NY, image seen); Ixtlán-Tuxtepec road, 21–23 km S of Valle Nacional (Km 82–84), 2200–2700 m, 26 Jul 1964, *J. T. Mickel 1465* (US, image seen); 76 km N of Ixtlán de Juárez on rte. 175, 5 km S of Vista Hermosa Campamento La Esperanza, 2800–1500 ft [850–460 m], 20 Sep 1973, *J. T. Mickel 7197* (UC!). Veracruz: Mpio. Catemaco, cerro Pipiapan, 500 m, 2 Apr 1984, *R. Acosta et al. 1521* (CIB!) (Fig. 1 D); Mpio. Catemaco, vertiente norte de la sierra de Santa Marta, 830 m, 10 Dec 1982, *R. Lira 174* (MEXU!); Mpio. Mecayapan, faldas del volcán Santa Marta, 1400 m, 22 Aug 2006, *T. Krömer & E. Otto 2942* (GOET!, MEXU!, UC!); Mpio. Pajapan, cerro San Martín Pajapan, 750–900 m, 3 Nov 1981, *M. Nee and J. I. Calzada 22735* (F, image seen); Mpio. San Andrés Tuxtla, ejido Ruiz Cortinez, falda del volcán San Martín Tuxtla, 1090 m, 17 Nov 2005, *T. Krömer et al. 2703* (MEXU!, UC!) (Fig. 1 E); Mpio. Totutla, Zacuapam, Aug 1931, *C. A. Purpus 15736* (UC!) (Fig. 1 F); Mpio. Zongolica, ejido de Zapaltecatl, 3600–2200 ft [1100–670 m], 21 Jun 1944, *J. V.*

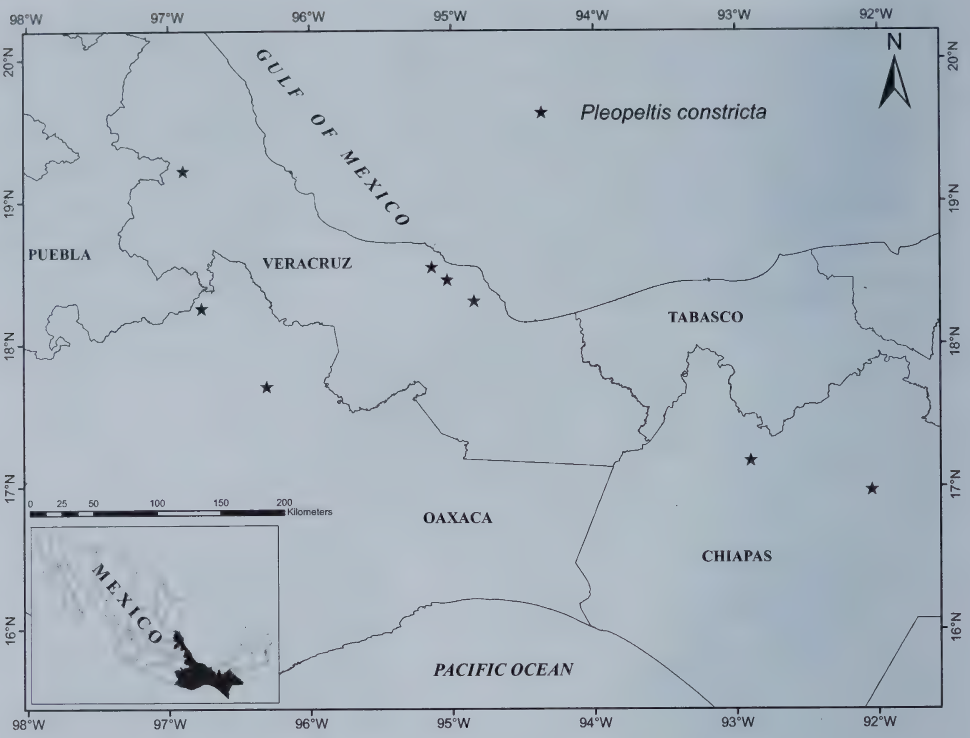

FIG. 3. Distribution map of *Pleopeltis constricta* in Mexico.

Santos 3055a (MICH, image seen); between Córdoba and Orizaba on Rte. 150, ca. 1200 m, 15 Aug 1960, *J. T. Mickel 746* (MICH, image seen).

Ecology: Epiphytic; in central and southeastern Veracruz in tropical humid and humid montane forests at 500–1400 m. In Oaxaca it occurs slightly lower at 450 m and up to 2200–2700 m.

Note: This new species was discussed in the PhD thesis of Sprunt (2010) in the context of a revision of specimens from the *Pleopeltis polypodioides* (L.) Watt complex.

2. *Aspidotis meifolia* (D. C. Eaton) Pic. Serm.

Specimen seen: Mpio. Las Minas, camino Cruz Blanca-Las Minas, km 16.5, 1400 m, 16 Mar 2005, *M. Vázquez et al. 8017* (CIB).

Ecology: Terrestrial or epipetric; in central Veracruz in pine-oak forests at 1400 m.

Note: *Aspidotis* includes two species in Mexico, one of which is endemic (*A. meifolia*). Although its occurrence in Veracruz was mentioned before by Villaseñor (2016), there is no voucher or reference to confirm this finding, which is the first record of this species and the genus within the state. It was previously reported from the neighboring states of San Luis Potosí and Tamaulipas (Mickel and Smith, 2004) and more recently from Hidalgo (Álvarez-Zúñiga *et al.*, 2011), so its presence in Veracruz was expected. The specimen cited here was collected in a transition zone between the Mexican Altiplano (Nearctic) and the humid forests of the south of the country (Neotropic).

3. *Asplenium juglandifolium* Lam.

Specimens seen: Mpio. Uxpanapa, ejido Progreso Chapultepec, 250 m, 19 Aug 2017, *T. Krömer et al. 4149* (UC); ibid., 145 m, 19 Aug 2017, *T. Krömer et al. 4160* (MEXU, UC).

Ecology: Epiphytic; in southern Veracruz in tropical lowland rainforests at 145–250 m.

Note: In Mexico, heretofore known only from a few collections from the neighboring state of Chiapas (Mickel and Smith, 2004). This new record increases the number of *Asplenium* species known from Veracruz to 45.

4. *Ceratopteris thalictroides* (L.) Brongn.

Specimen seen: Mpio. Uxpanapa, ejido Progreso Chapultepec, 110 m, 19 Aug 2017, *T. Krömer et al. 4168* (MEXU, UC).

Ecology: Aquatic plant rooted in mud, in shallow water of slow moving rivers or streams; in southern Veracruz in tropical lowland rainforests at 110 m.

Note: In Mexico, known previously only from a few collections from the state of Guerrero. With this new record, both *Ceratopteris* species reported from Mexico occur in Veracruz.

5. *Elaphoglossum lanceum* Mickel

Specimen seen: Mpio. Acajete, El Encinal, 2500 m, 15 Mar 2015, *V. Guzmán-Jacob et al. 373* (UC).

Ecology: Epiphytic; in central Veracruz in pine-oak forests at 2500 m.

Note: In Mexico previously known only from a few collections made in the neighboring state of Oaxaca. Five new records of *Elaphoglossum* were reported by Krömer *et al.* (2015), increasing the number known from Veracruz to 33.

6. *Hemionitis levyi* E. Fourn.

Specimen seen: Mpio. Puente Nacional, barranca de La Palmilla, 590 m, 8 Aug 2015, *C. I. Carvajal-Hernández et al. 1060* (CIB, MEXU).

Ecology: Terrestrial; in coastal Veracruz in tropical humid forests at 590 m.

Note: This is the first record of this species on the Atlantic slope in Mexico. It was very scarce at the collecting site, where it survived in a fragment of forest vegetation in a ravine surrounded by citrus plantations.

7. *Ophioglossum crotalophoroides* Walter

Specimen seen: Mpio. San Juan Evangelista, 3 km al sur del poblado de La Cercilla, 100 m, 6 Sep 2017, *L. Rosas and H. Bojórquez 07* (CIB).

Ecology: Terrestrial; in southern Veracruz in secondary vegetation derived from tropical oak forest at 100 m.

Note: This species is widely distributed in Mexico; however, this is the first record in the country from low elevation; previously recorded between 1000–3350 m (Mickel and Smith, 2004).

8. *Pecluma chiapensis* (A. M. Evans & A. R. Sm.) M. G. Price

Specimen seen: Mpio. Uxpanapa, ejido Progreso Chapultepec, 170 m, 18 Aug 2017, *T. Krömer et al. 4120* (MEXU, UC).

Ecology: Epiphytic; in southern Veracruz in tropical lowland rainforests at 170 m.

Note: This species is endemic to Mexico, where it was known only from Oaxaca and Chiapas. In Veracruz, it occurs in the region of Uxpanapa at the border zone to the aforementioned states. *Pecluma* was first defined by Price (1983), who transferred 29 species into his new genus; nearly all of them except *P. chiapensis* had been treated by Evans (1969) as members of the *Polypodium pectinatum-plumula* group. *Pecluma* has now been expanded to accommodate a number of additional species from the Neotropics (e.g., Kessler and Smith, 2005; Assis *et al.*, 2016). *Pecluma chiapensis* was treated by Smith (1981) and by Mickel and Smith (2004) in *Polypodium*, where first described, but was transferred by Price (1983) to *Pecluma*. It is now clear that this rarely collected species is indeed properly placed in *Pecluma* because of its narrow, closely-placed pinnae, thin blade texture, rhizome scales, and habit, lax whitish hairs to 1 mm long on laminar surfaces (as on some other spp. of *Pecluma*). It resembles *Pecluma hartwegiana* (Hook.) F. C. Assis & Salino. Molecular support for *P. chiapensis* is desirable but not yet available.

9. *Polytaenium chlorosporum* (Mickel & Beitel) E. H. Crane

Specimen seen: Mpio. Uxpanapa, ejido Progreso Chapultepec, 130 m, 19 Aug 2017, *T. Krömer et al. 4145* (MEXU, UC).

Ecology: Epiphytic; in southern Veracruz in tropical lowland rainforests at 130 m.

Note: In Mexico, previously known only from a few collections in the neighboring states of Chiapas and Oaxaca. With this new record, all four *Polytaenium* species reported for Mexico in Mickel and Smith (2004) are known from Veracruz.

For the following two species, heretofore known from Veracruz, we propose new combinations:

1. ***Pecluma liebmannii*** (C. Chr.) A. R. Sm. & Carv.-Hern., **comb. nov.**

Basionym: *Polypodium liebmannii* C. Chr., Index Filicum 539. 1906.

Type:—MEXICO. Puebla: Chinautla, *Liebmann s.n.* [Pl. Mex. 2525; Fl. Mex. 125, 715] (Holotype: C, fragm. US; Isotypes: K, P).

Specimens seen: Mpio. Acajete, El Encinal, 2500 m, 10 May 2015, *V. Gúzman-Jacob et al. 550* (UC); Mpio. Yecuatla, 1 km al sur de la comunidad "La Unión", 1000 m, 20 Nov 2009, *C. I. Carvajal-Hernández 214* (CIB).

Ecology: Epiphytic; in central Veracruz in humid montane and pine-oak forests at 1000–2500 m.

Note: This species is endemic to Mexico, where it was recorded in moist oak forests between 1700–2150 m in Hidalgo, Puebla, and Veracruz (Mickel and Smith, 2004). Recently, it was reported from a secondary forest derived from humid montane forest at the Sierra de Chiconquiaco in central Veracruz (Carvajal-Hernández, Krömer, and Vázquez-Torres, 2014). Although previously treated in *Polypodium,* we consider *Pecluma liebmannii* to be closely allied to *Pecluma hartwegiana* (Hook.) F. C. Assis & Salino, differing by the more numerous longer hairs on the stipes and rachises, these 0.5–1.5 mm long (vs. glabrous stipes and hairs to 0.3 mm long in *P. hartwegiana*), dense laminar hairs, both abaxially and adaxially (vs. lamina hairs scattered) (see Mickel and Smith, 2004, who treated both species in *Polypodium*).

2. ***Pleopeltis acicularis*** (Weath.) A. R. Sm. & T. Krömer, **comb. nov.**

Basionym: *Polypodium polypodioides* (L.) Watt var. *aciculare* Weath., Contr. Gray Herb. 124:33. 1939.

Type:—COSTA RICA. San José: Rio Torres near San Francisco de Guadalupe, 1170 m, *A. Tonduz 8476* (Holotype: GH 00021884, fragm. US 2084281; Isotypes: BR 697769, CR, F 71487, NY 00144894).

Specimens seen: Mpio. Atzalan, carretera Atzalan-Tlapacoyan, 1400 m, 13 Mar 2015, *C. I. Carvajal-Hernández et al. 982* (CIB), comunidad Cruz Gorda, congregación San Salvador, 1100 m, 18 Jun 2008, *T. Krömer et al. 3406* (MEXU, UC); Mpio. Coacoatzintla, cerro de Coacoatzintla, 1550 m, 7 Jul 1992, *M. A. Smith and A. Fernández 232* (CIB); Mpio. Emiliano Zapata, Chavarillo, 1000 m, 25 Jul 2014, *V. Gúzman-Jacob et al. 318* (UC); Mpio. Las Minas, cerca de la Planta Hidroeléctrica, 1430 m, 19 Mar 2015, *C. I. Carvajal-Hernández et al. 989* (CIB); Mpio. San Andrés Tuxtla, Estación de Biología Tropical "Los Tuxtlas", cerro Vigía 5, 450 m, 12 Apr 2005, *T. Krömer et al. 1925* (GOET, MEXU, UC), ejido Balzapote, 45 m, 4 Ago 2005, *T. Krömer et al. 2452* (GOET, MEXU, SEL, XAL); Mpio. Uxpanapa, entre La Esmeralda y Poblado Cinco, 100 m, 16 Nov 2005, *T. Krömer et al. 2677* (MEXU, UC); Mpio. Xalapa, camino de Chiltoyac a Paso San Juan, 600 m, 23 Feb 2007, *C. I. Carvajal et al. 39* (CIB).

Ecology: Epiphytic; in central Veracruz in tropical humid, tropical semideciduous, humid montane and pine-oak forests, as well as in citrus and shaded coffee plantations at 45–2500 m.

Note: This species is widely distributed in Mexico and Central America. It has usually been treated as *Polypodium polypodioides* var. *aciculare* (e.g., by Mickel & Smith, 2004); however, our study, as well as unpublished work by Sprunt (2010), suggest that molecular and morphological differences are of sufficient magnitude that var. *acicularis* should be elevated to species rank. We include the Mexican states of Chiapas, Sinaloa, and Tabasco in the range, as additions to the distribution given by Mickel and Smith (2004), because of recent annotations by Sprunt and the synonymization of *Polypodium polypodioides* var. *knoblochianum* Mickel under *Pleopeltis acicularis* by Sprunt (2010).

Discussion

The nine new fern records and a recent new species (Sundue, 2017) bring the new total for the state of Veracruz to 574 species (Krömer *et al.*, 2015). Veracruz is the third richest Mexican state in terms of total fern diversity. It is likely that Veracruz will reach about 600 confirmed species within the next decade, as there are still botanically mostly unexplored areas with humid tropical and montane forests (Krömer *et al.*, 2015). Thus, a two-day collecting trip to the Uxpanapa region in 2017 revealed four new state records. Other regions of specific interest are the montane areas of the sierras de Zongolica and Huayacocotla, located in central and northern Veracruz, respectively.

The highest generic species richness in Veracruz is found in *Asplenium* (45 species), with one new record reported herein. Our new record in *Elaphoglossum* increases the number of species in the state to 33; previously, Krömer *et al.* (2015) reported five new state records for that genus, and Carvajal-Hernández *et al.* (2018) recently found four new records for the same genus in Tabasco. These findings demonstrate that our knowledge of the national distribution of those ferns is still incomplete.

Most of the present new state records were collected either in the tropical lowland rainforests of the Uxpanapa region or in the mountainous area of central Veracruz. Both regions are of great importance for the plant diversity of Veracruz. The latter represents the region with the highest diversity of fern species in Veracruz (Tejero-Díez *et al.*, 2011), as it is located in the transition zone between the Nearctic and Neotropical regions. Thus, it includes species of the former area such as *Aspidotis meifolia*, as well as species with tropical affinity such as *Asplenium hostmannii*, *Elaphoglossum lanceum*, and *Hemionitis levyi*. On the other hand, the southern lowland region of Uxpanapa, which borders with Chiapas and Oaxaca, represents a very biodiverse area in general and is considered a refuge for the vascular flora in the Cenozoic, where several endemic plant species have been described (Gómez-Pompa, Krömer, and Castro-Cortés, 2010; Jimeno-Sevilla *et al.*, 2018; Wendt, 1989). However, ferns have been poorly studied in this region, and the only relevant work was carried out by Riba and Pérez-García (1979), reporting 69 species.

Veracruz is one of the states with the highest deforestation rates in Mexico (Ellis, Martínez-Bello, and Monroy-Ibarra, 2011). This situation affects biodiversity in general and ferns in particular. Ecosystems such as humid montane and also lowland forests have undergone considerable loss of fern species due to anthropogenic disturbances (Carvajal-Hernández, Krömer, and Vázquez-Torres, 2014; Carvajal-Hernández *et al.*, 2017). Consequently, some regions like Uxpanapa, Zongolica, and Huayacocotla require urgent exploration and conservation programs, as there are still many undiscovered species that may be highly endangered by the ongoing deforestation and habitat loss.

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Eight New Taxa of *Hypolepis* (Dennstaedtiaceae) from the Neotropics

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Abstract.—Seven new species and one new variety of *Hypolepis* are presented, bringing the total recognized for the genus in the Neotropics to about 50 species (and a total of 60 taxa). The new taxa include *H. barringtonii* (endemic to Florida, U.S.A.), *H. cubensis* (endemic to Cuba), *H. feeana* (from Colombia, Venezuela, and the Antilles), *H. zimmerae* (from Costa Rica, Colombia, Ecuador, and Peru), *H. sunduei* (endemic to Peru), *H. forzzae* (endemic to Amazonas, in the border of Brazil and Venezuela), *H. miodelii* (endemic to Rio de Janeiro, Brazil), and *H. rigescens* var. *paranaensis* (endemic to Paraná, Brazil). All new taxa are described, illustrated, and discussed. Treatments of *H. flexuosa* and *H. stuebelii* are provided because the description of *H. zimmerae* and *H. feeana* alters their circumscription, respectively. It is also suggested that *H. repens* does not occur in Florida, Cuba, nor Jamaica.

Key Words.—Antilles, Central America, *Hypolepis repens, Hypolepis stuebelii,* South America

Hypolepis Bernh., as recently circumscribed by Shang *et al.* (2018), is a monophyletic genus placed in the "Hypolepidoid" clade of the Dennstaedtiaceae. It is recognized by the branched, long-creeping rhizomes to 30 m long, medium to large leaves up to 7 m long, commonly provided with prickles (= aculei) and catenate hairs on petioles and rachises, 2–5-pinnate blades, and marginal, discrete sori either protected by adaxial indusia or not. It is especially diverse in the tropics, but a few species also extend into temperate zones, especially in the southern hemisphere (*e.g.,* Brownsey and Chinnock 1984, Kramer, 1990; Schwartsburd and Prado, 2015; Tryon and Tryon, 1982).

Previous workers have estimated that the worldwide species richness of *Hypolepis* ranges from about 40 to 50 species. Of these, 15 to 20 species were recorded for the Americas (Kramer, 1990; Mickel and Smith, 2004; Moran, 1995; Tryon and Tryon, 1982). Through a careful study of herbarium specimens, Schwartsburd and Prado (2014, 2015, 2016) suggested that there were about twice as many species as previously thought. In South America alone they recognized 25 species and a total of 30 taxa (including subspecies, varieties, and hybrids).

Schwartsburd and Prado (2015, 2016) provided the first contributions to a modern taxonomic revision of *Hypolepis* for South America, contributing substantially to the understanding of the genus (including description of new taxa, new circumscriptions, lectotypifications, and new distributional data).

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Realizing that some rare and local-endemic taxa had been overlooked, Schwartsburd *et al.* (2017) later described two new endemic species from Bolivia and re-circumscribed another two taxa, bringing the number to 28 species and a total of 34 taxa for South America. With the new generic arrangement of Shang *et al.* (2018), these numbers were respectively reduced to 27 and 33—*Hypolepis nigrescens* Hook. was combined into the newly described *Hiya* Hui Shang.

The main difficulty in studying *Hypolepis,* as well as other genera of ferns with large leaves, is that herbarium materials are often fragmentary. For some species with four-meter tall leaves and quadripinnate blades there is only a piece of a pinnule available, sometimes badly preserved or over-dried—problems also recognized by Brownsey and Chinnock (1984, on page 46), Moran (1995, on page 153), and Schwartsburd and Prado (2015, on page 268). The result is a serious lack of information about rhizomes, habit, growth pattern and size of leaves, petiole color and prickle development, blade dissection, and indument; the result is that taxa deserving recognition remain unknown to science.

My recent work with an array of herbarium specimens from a number of institutions leads me to conclude that there remain undescribed local-endemic taxa from South America, especially from regions with one or only a few collections available. These endemic taxa are here described. I also proposed narrower circumscriptions for *H. flexuosa* Sodiro and *H. stuebelii* Hieron., by segregating as new species *H. zimmerae* Schwartsb. and *H. feeana* Schwartsb. In addition, I also describe two new local-endemic species, one from Florida and another from Cuba, previously included in *H. repens* (L.) C. Presl. Consequently, I provide an updated account of the geographic distribution of *H. repens*.

The novelties presented here added to the main recent literature reveal ca. 50 taxonomically valid species of *Hypolepis* from the Neotropics, with a total of ca. 60 taxa, including subspecies, varieties, and hybrids (Shang *et al.* 2018; Mickel and Smith, 2004; Moran, 1995; Nauman, 1993; Proctor, 1977, 1985, 1989; Rojas-Alvarado, 2001; Schwartsburd and Prado, 2014, 2015, 2016 and references therein; Schwartsburd *et al.,* 2017).

MATERIALS AND METHODS

Specimens from herbaria A, B, BM, BR, CESJ, FI-PS, G, GH, K, L, LE, NY, OXF, R, RB, SP, U, UC, US, VEN, VIC, VT, and W were analyzed. Reinaldo Pinto drew figures 1, 2A, E–H, 3, and 4; Kley Souza drew figures 2B–D.

Sorus developement was based on the interpretations of Schölch (2000) (and Bower, 1928), in which there is a "displacement of the marginal initials towards" the abaxial surface of blades. Thus, according to this interpretation, the sori develop from the leaf marginal initials, but later appear to be abaxial. In this taxonomic treatment, I refer to sori as either marginal (= adjacent to the margin on the abaxial surface) or submarginal (= abaxial and away from the leaf margin). The length of the indusia (*i.e.,* in the orientation of veins) may be

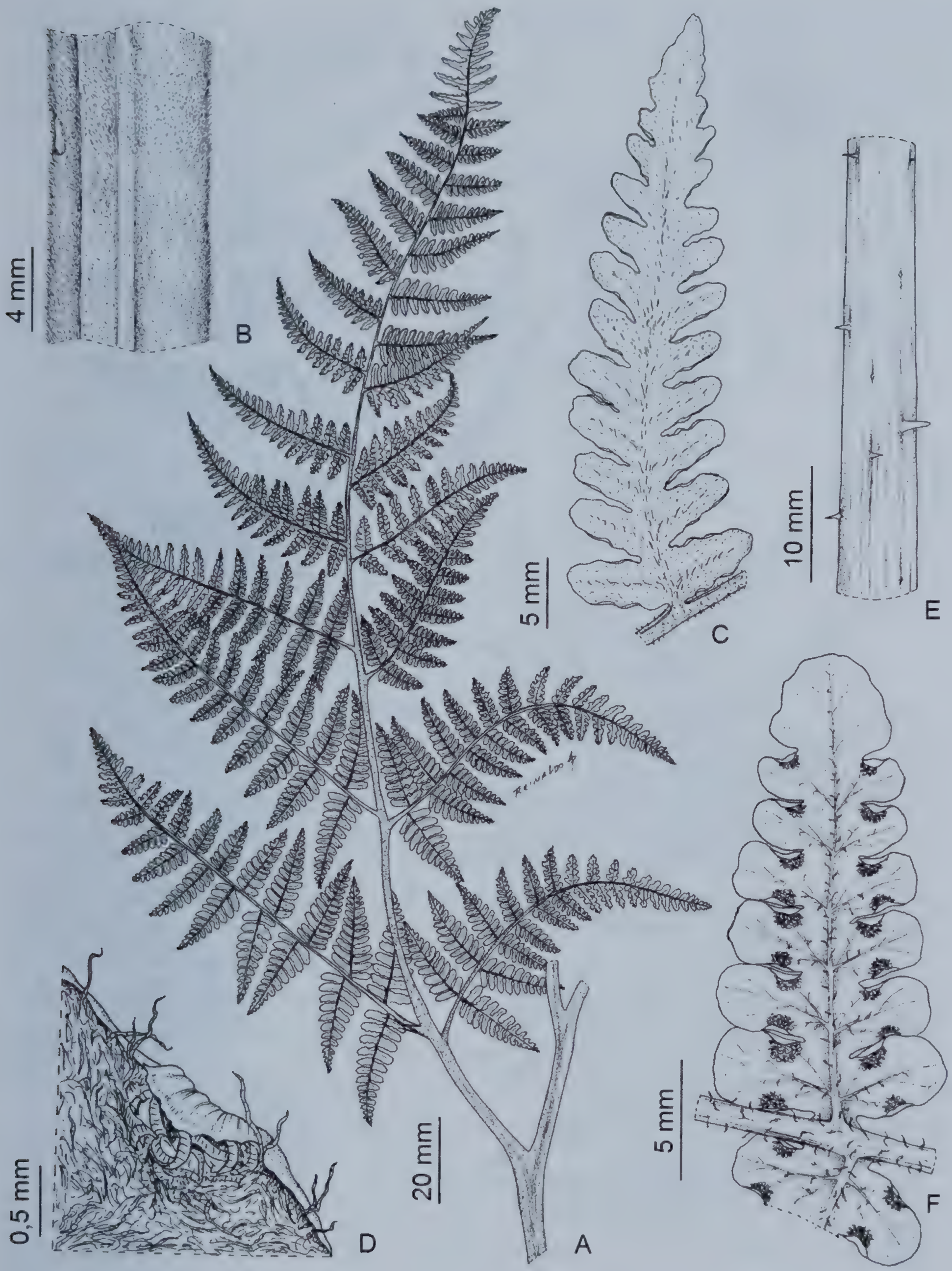

FIG. 1. A–D *Hypolepis zimmerae* (*van der Werff 25433*). A. Basal pinna. B. Petiole, showing indument. C. Segment, abaxially. D. Detail of sorus, indusium, and tomentose laminar tissue between the veins. E–F *Hypolepis cubensis* (*Wright 894*). E. Petiole, showing aculei. F. Secondary pinnule, abaxially.

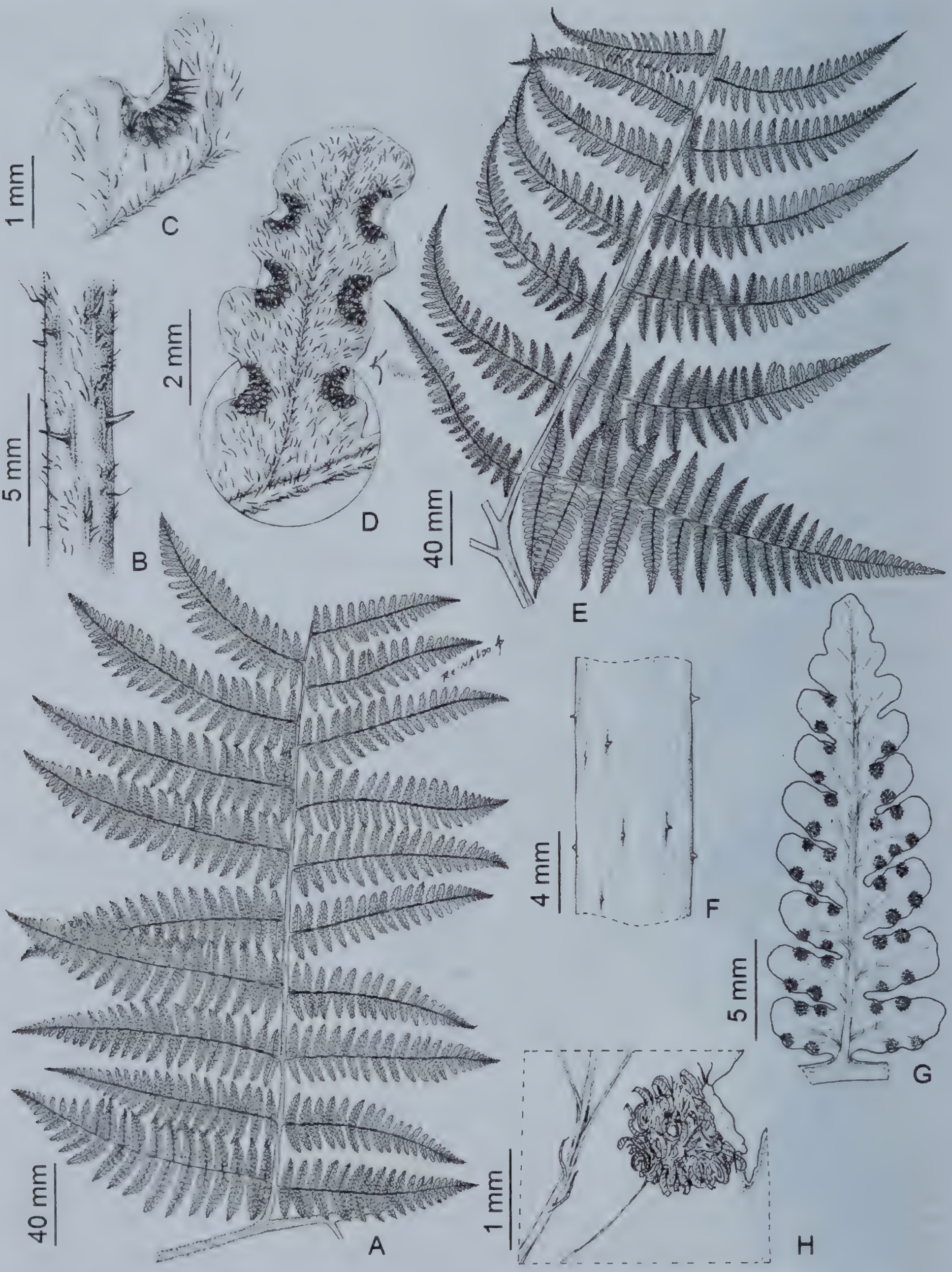

FIG. 2. A–D *Hypolepis feeana* (*Ortega 1640*). A. Basal pinna. B. Rachis, showing aculei and hairs. C. Detail of sorus and indusium. D. Segment, abaxially. E–H *Hypolepis forzzae* (*Forzza 7277*). E. Basal pinna. F. Petiole, showing aculei. G. Secondary pinnule, abaxially. H. Detail of sorus and indusium.

variable according to the stage of soral development, and is determined to not be taxonomically informative. On the other hand, indusium width (*i.e.*, accompanying the lamina margin) is stable and taxonomically informative. In the descriptions, only the width is provided.

RESULTS AND DISCUSSION

New species from Florida and Cuba, and comments on Hypolepis repens

Hypolepis barringtonii Schwartsb., ***spec. nov.*** TYPE.—UNITED STATES OF AMERICA. **Florida:** Clay County, Keystone Heights, 29.834°N, 81.949°W, 65 m, 17 Jun 2018, *W.L. Testo 1615* (holotype: VT-on 2 sheets; isotype: FLAS-*n.v.*).

Diagnosis.—Differs from *Hypolepis repens* by the shorter leaves, to 1.5 m long (*vs.* to 4 m), membranaceous blades (*vs.* chartaceous), and sparsely aculeate petioles and rachises (*vs.* densely aculeate).

Plants terrestrial. *Rhizomes* 1.5–2.5 mm diam., glabrescent; *the hairs* catenate-acicular, yellowish brown, 2–3 mm long, 20–30-celled. *Leaves* determinate, 0.35–1.5 m long; *petioles* 10–60 cm × 1.5–2 mm, reddish brown proximally, lighter brown to stramineous distally, rugose, sparsely aculeate, abaxially glabrescent, adaxially pilose to glabrescent, the *aculei* straight, to 1 (–1.5) mm long, the *hairs* catenate-acicular, 0.5–1.5 mm long, 5–15-celled; *blades* tripinnate-pinnatifid proximally, 30–100 × 30–80 cm, membranaceous; *rachises* straight, stramineous, sparsely aculeate, rugose abaxially and adaxially with hairs similar to those from the petioles; *basal pinnae* 15–40 × 7–20 cm, subequilateral; *costae* pilose to glabrescent abaxially and adaxially, the hairs similar to those from the petioles and rachises; *costules* sparsely pilose to glabrescent abaxially and adaxially, the hairs shorter, to 0.7 mm long, to 7-celled; *veins* sparsely pilose to glabrescent abaxially, glabrous adaxially; *laminar tissue between the veins* glabrous abaxially and adaxially; *lamina margins* glabrous; *sori* abaxial-marginal; *indusia* reflexed, partly covering the sori, entirely greenish or proximally greenish and distally hyaline, the *margins* smooth, glabrous.

Iconography.—See drawings of "*Hypolepis repens*" in Nauman (1993).

Distribution and ecology.—Endemic to Florida, U.S.A.; from sea level to ca. 100 m.

Etymology.—The specific epithet honors Dr. David Stanley Barrington (1948–), professor at the University of Vermont, and curator of the Pringle herbarium (VT). Barrington is an active researcher of taxonomy, phylogeny, and hybridization of ferns, especially *Polystichum*.

Specimens examined.—UNITED STATES OF AMERICA. **Florida:** St. Leo, Tasco County, 1925, *H. O'Neill s.n.* (FI-PS); near DeSoto City, 20 May 1925, *J.K. Small & E.T. Wherry 12637* (K); Orange County, near Zellwood, 20 May 1925, *E.J. Palmer 27455* (K); Highlands County, Sweet Bay hammock, 12 Jan 1925, *J.K. Small & P. Matthaus 11638* (LE); County Highlands, southeast of Childs, 8

Feb 1836, *D.S. Correl 6165* (FI-PS, MO-*n.v.*); Polk County, Lake Pierce, Mar 1986, *A.M. Evans 3410* (U); Osceola County, hammock, 13 Mar 1969, *G.R. Cooley et al. 12635* (LE); Oveido, 1908, *J.C. Armstrong s.n.* (VT-192240); Oveido, 1908, *J.C. Armstrong s.n.* (VT-192241); Oveido, 1908, *T. Mead s.n.* (VT-192238); Oveido, 1910, *Anonymous s.n.* (VT-192239); Springlake, Hernando County, 10 Mar 1935, *M. Brown s.n.* (VT-192242).

According to Nauman (1993), *Hypolepis barringtonii* (cited as "*Hypolepis repens*") has a mitotic chromosome number of 2n= 208, which makes it a tetraploid taxon. Nauman (1993) described its indument as "glandular-pubescent", but I did not find any glandular hairs in the examined specimens.

Hypolepis cubensis Schwartsb., ***spec. nov.*** TYPE.—CUBA. Prope villam Monte Verde dictam, Cuba Orientali, Jan–Jul 1859, *C. Wright 894* (holotype: K! [ex Herb. incognitum]; isotypes: BR!, BM!, GH!-00934336, K! [ex Herb. Hooker], L!, LE!-on 2 sheets, NY!-01903303, NY!-01903318, NY!-01903319, NY!-01903320, NY!-01903391 [overwritten as "895 *p.p.*"], W!). **Figs. 1E, F.**

Diagnosis.—Differs from *Hypolepis repens* by the wider, stramineous indusia to 1.2 mm wide (*vs.* hyaline indusia to 0.5 mm wide).

Plants terrestrial. *Rhizomes* 2–3.5 mm diam.; *the hairs* catenate-acicular, yellowish brown, 2–3 mm long, 20–30-celled. *Leaves* determinate, more than 2 m long (complete leaves not seen); *petioles* to 140 cm × 3–5 mm, dark brown proximally, lighter brown distally, rugose, densely aculeate, glabrescent, with trichomidia, the *aculei* straight, to 1.5 mm long, the *hairs* catenate-acicular, 0.3–0.6 mm long, 4–8-celled; *blades* tripinnate-pinnatifid to quadripinnate proximally, at least 1.5 × 0.9–1.4 m (complete leaves not seen), herbaceous; *rachises* straight, stramineous to light brown, abaxially with trichomidia, adaxially with hairs and trichomidia, aculeate, non-rugose; *basal pinnae* 45–70 × 20–30 cm, subequilateral; *costae* pilose abaxially, glabrescent adaxially, the hairs similar to those on the petioles and rachises; *costules* glabrescent abaxially, glabrous adaxially; *veins* glabrous both abaxially and adaxially; *laminar tissue between the veins* glabrous abaxially and adaxially; *lamina margins* glabrous; *sori* abaxial-marginal; *indusia* reflexed, stramineous, 0.8–1.2 mm wide, the *margins* crenate, glabrous.

Distribution and ecology.—Endemic to Cuba; from ca. 600–1000 m.

Etymology.—The specific epithet represents the distribution of the taxon, which is endemic to Cuba.

Specimens examined.—CUBA. **Santiago de Cuba:** El Cobre, Sierra Maestra, Loma del Gato et environs, 950 m, 1924, *F. Clément 138b* (BM). **[Province Unknown]:** Oriente, La Perla to Pinales de Monte Verde, 660 m, 16 Feb 1911, *J.A. Schafer 8851* (A-on 2 sheets, K); in Cuba orientali, 1856–1857, *C. Wright 65* (NY).

Hypolepis repens is morphologically homogeneous throughout its range, from southern Mexico (ca. 17°N) and Hispaniola (ca. 19°N) southwards to Bolivia (ca. 17°S), Paraguay (ca. 22°S), and Brazil (in São Paulo and Rio de

Janeiro, ca. 22°S). Specimens from Florida, Cuba, and Jamaica, commonly identified as *H. repens* consistently differ from *H. repens s. str.* They are better regarded as three local-endemic species, including two new ones described above and *H. jamaicensis* Maxon ex Proctor.

Hypolepis repens s. str. as redefined here is characterized by leaves to 4 m long, petioles and rachises densely aculeate, with aculei up to 4 mm long, the petioles to 8(–10) mm diam., proximally dark brown and distally lighter brown, chartaceous blades, laminar axes with catenate-acicular hairs and trichomidia, veins abaxially with sparse catenate-acicular hairs to glabrescent, glabrous laminar tissue between the veins, and narrow, hyaline indusia, 0.4–0.5 mm wide, with smooth to slightly crenate, glabrous margins (see Schwartsburd and Prado 2015, Figs. 15A–E).

In contrast to *Hypolepis repens s.str.*, *H. barringtonii* has much shorter leaves, no more than 1.5 m long, sparsely aculeate petioles and rachises (seeming virtually non aculeate), the aculei to 1(–1.5) mm long, the petioles to 2 mm diam. and proximally reddish-brown, and membranaceous blades (see figure in Nauman 1993).

Hypolepis cubensis differs from *H. repens s. str.* by shortly aculeate petioles and rachises, the aculei to 1.5 mm long (*vs.* to 4 mm), glabrous veins abaxially (*vs.* with catenate-acicular hairs), and, especially, by the much wider and stramineous indusia, 0.8–1.2 mm wide (*vs.* hyaline, to 0.5 mm wide) (Figs. 1E, F).

Hypolepis jamaicensis is characterized by densely pubescent veins and broad indusia, with dentate, sparsely hairy margins (see also Proctor, 1985).

New species from the Andean region (and Antilles), and new circumscriptions for Hypolepis flexuosa and H. stuebelii

Hypolepis feeana Schwartsb., ***spec. nov.*** TYPE.—[HISPANIOLA]. **Santo Domingo:** s.d., *F.R.C. de Tussac s.n.* (holotype: RB!-120408 [ex Herb. Fée]). **Figs. 2A–D.**

Diagnosis.—Differs from *Hypolepis stuebelii* by petioles and rachises copiously aculeate, with aculei to 4 mm long; also by the herbaceous, concolorous, quadripinnate-pinnatifid blades, and sub-equilateral basal pinnae.

Plants terrestrial. *Rhizomes* not seen. *Leaves* determinate, to 3.5 m long at least (complete leaves not seen); *petioles* to 1 m long at least (complete leaves not seen), to 8 mm diam, proximally reddish brown, distally golden brown, rugose, densely aculeate, abaxially and adaxially hirsute, the *aculei* conspicuous, straight, to 4 mm long, the *hairs* acicular, erect. 0.15–0.25 mm long, 2–3(–4)-celled; *blades* proximally quadripinnate-pinnatifid, to 2.5 m long at least, to 2.4 m large at least (complete leaves not seen), herbaceous; *rachises* straight, golden brown, rugose, aculeate, hirsute-villous abaxially and adaxially with three kinds of hairs, *the first kind of hair* similar to those from petioles, *the second kind of hair* catenate-acicular, 0.7–1.5 mm long, 7–15-celled, *the third kind of hair* catenate-glandular, 0.3–1 mm long, 5–15-

celled; *basal pinnae* to 1.2 m × 75 cm, subequilateral; *costae* with the same indument as the rachises or rarely the first kind of hair absent; *costules* abaxially copiously hirsute, with the first kind of hair conspicuous, the second and third kinds sparse or absent, adaxially with only the second and third kinds of hair, these sparse; *veins* abaxially hirsute with the first kind of hair conspicuous and a few hairs of the third kind, adaxially glabrescent; *laminar tissue between the veins* abaxially hirsute with the first kind of hair conspicuous and a few hairs of the third kind, adaxially glabrous; *lamina margins* glabrous; *sori* abaxial-marginal; *indusia* reflexed, proximally greenish, distally hyaline, the margins copiously hairy.

Distribution and ecology.—Jamaica, Hispaniola, and east of the Andes in Colombia and Venezuela; from 300 to 1750 m.

Etymology.—The specific epithet honors late French pteridologist Antoine Laurent Apollinaire Fée (1789–1874). Fée provided innumerable contributions to Pteridology, mainly through his works entitled *Mémoires sur les familles des fougéres.*

Specimens examined.—JAMAICA. **Cinchona:** Below New Haven Gap, 2–10 Sep 1906, *L.M. Underwood 3158* (B, NY-on 2 sheets). **Department Unknown:** Blue Mts., Big Gulley Way, to Vinegar Hill, ca. 3500 ft, 22 May 1916, *J.R. Perkins 1171* (B, GH, K); From St, Helen's Gap to Latimer river, 1400–1475 m, 9 Mar 1920, *W.R. Maxon & E.P. Killip 898* (GH).

HISPANIOLA. **Santo Domingo:** Prov. de Samaná, Sánchez, road to La Terriena, ca. 300 m, 25 Apr 1930, *E.L. Eckman, Pl. Ind. Occid. H 14753* (BM, K, NY, S-*n.v.*).

VENEZUELA. **[Aragua]:** P.N. Aragua, 1000–1100 m, 2 Dec 1938, *L.L. Williams & A.H.G. Alston 190* (BM-on 2 sheets); Prope Coloniam Tovar, [seaside of mountain range between Petaquire and the sea, also farther west], 3000 ft, 1858, *A. Fendler 431* (B, GH, K, MO-*n.v.*, YU-*n.v.*). **[Distrito Capital]:** Caracas, 1842, *J.J. Linden, mixtum cum 245* [*245b*] (BM). **Lara:** Morán, 1500 m, 6 Mar 1983, *F. Ortega et al. 1640* (NY, VEN).

COLOMBIA. **Nariño:** Near Riocuarte, 1500 m, 7 May 1939, *A.H.G. Alston 8430* (BM); Riocuarte, Chucunés, Res. Nat. La Planada, 01°06′N, 77°54′W, 1750 m, 18 May 1991, *S.P. Churchill et al. 18237* (NY-on 3 sheets). **Santander:** Vicinity of El Roble, 1500 m, 16 Feb 1927, *E.P. Killip & A.C. Smith 19368* (GH, NY).

Here I propose the segregation of *Hypolepis feeana* from *H. stuebelii,* suggesting a narrower circumscription for this species. *Hypolepis stuebelii s. str.* occurs west of the Andes, in Colombia, Ecuador, and Peru. In comparison, *H. feeana* occurs around the Caribbean Sea and east of the Andes, in Jamaica, Hispaniola, Colombia, and Venezuela. Plants from Jamaica, previously determined as *H. stuebelii* by Proctor (1985), are better named *H. feeana;* plants from Costa Rica determined as *Hypolepis stuebelii* by Moran (1995), are either *H. grandis* Lellinger or *H. moraniana* A. Rojas.

In addition to geographical distribution, *Hypolepis feeana* differs from *H. stuebelii s. str.* by the copiously aculeate petioles and rachises, the aculei to 4 mm long, herbaceous, concolorous, quadripinnate-pinnatifid blades, subequilateral basal pinnae, and wide indusia, fully covering the sori (Figs. 2A–D). On the other hand, *H. stuebelii s. str.* has shortly aculeate petioles and rachises, the aculei are 0.5–1(–1.5) mm long, the blades are chartaceous to subcoriaceous, bicolorous, and tripinnate-pinnatifid (to quadripinnate), the basal pinnae are equilateral, and the indusia are short, only partly covering the sori (Figs. 4C–F).

Hypolepis stuebelii Hieron. **Figs. 4C–F.**

Plants terrestrial. *Rhizomes* 3–4.5 mm; *the hairs* catenate-acicular, reddish-brown, 2–3(–5) mm long, 20–30-celled. *Leaves* determinate, to 4 m long (complete leaves not seen); *petioles* to 1.8 m × 7 mm, golden brown, rugose, shortly aculeate, abaxially and adaxially hirsute, the *aculei* straight, 0.5–1(–1.5) mm, the *hairs* (first kind) acicular, hyaline, erect. 0.15–0.25 mm long, 2–3(–4)-celled; *blades* proximally tripinnate-pinnatifid to quadripinnate, chartaceous to sub-coriaceous, to 2.2 × 1.6 m; *rachises* straight, golden brown, rugose, aculeate, hirsute-villous abaxially and adaxially, with three kinds of hair, the *first kind of hair* similar to those from petioles, the *second kind of hair* catenate-acicular, 0.7–1.5 mm long, 7–15-celled, the *third kind of hair* catenate-glandular, 0.3–1 mm long, 5–15-celled; *basal pinnae* equilateral, 50–80 × 20–40 cm; *costae* with the same indument of the rachises, rarely the first kind of hair absent; *costules* abaxially copiously hirsute, with the first kind of hair much conspicuous, the second and third kinds sparse, adaxially with only the second and third kinds of hair, these sparse; *veins* abaxially hirsute with the first and the third kinds of hair, the third kind shorter, to 0.3 mm long, adaxially glabrescent; *laminar tissue between the veins* abaxially hirsute, with the same indument pattern of the veins, adaxially glabrous; *lamina margins* glabrous; *sori* abaxial-marginal; *indusia* reflexed, partly covering the sori, hyaline, the *margins* copiously hairy.

Distribution and ecology.—West of the Andes, in Colombia, Ecuador, and Peru; from 500 to 1900 m.

Hypolepis zimmerae Schwartsb., ***spec. nov.*** Type.—COLOMBIA. **[Cauca]:** Páramo de las Delicias, Central Andes von Popayan, 3200–3500 m, s.d., *F.C. Lehmann 4441* (holotype: B!-200074637; isotypes: K!-on 2 sheets, NY!-03376891). **Figs. 1A–D.**

Diagnosis.—Differs from *Hypolepis flexuosa* by shorter leaves, to 2 m long; and by densely tomentose petioles, laminar axes, and abaxial surface of blades.

Plants terrestrial. *Rhizomes* 3–6 mm diam.; *the hairs* catenate-acicular, yellowish brown, 0.3–0.6 mm long, 6–12-celled. *Leaves* with intermittent growth, scandent, 0.6–2 m long; *petioles* 30–100 cm × 4–12 mm, reddish brown, inermous, rugose, densely tomentose, the *hairs* catenate-acicular, 5–10-celled, 0.4–0.7 mm long, commonly with reddish tips; *blades* proximally tripinnate-pinnatifid to pentapinnate, ca. 30–120 × 40–100 cm, coriaceous; *rachises* flexuous, proximally reddish brown, distally light brown, inermous,

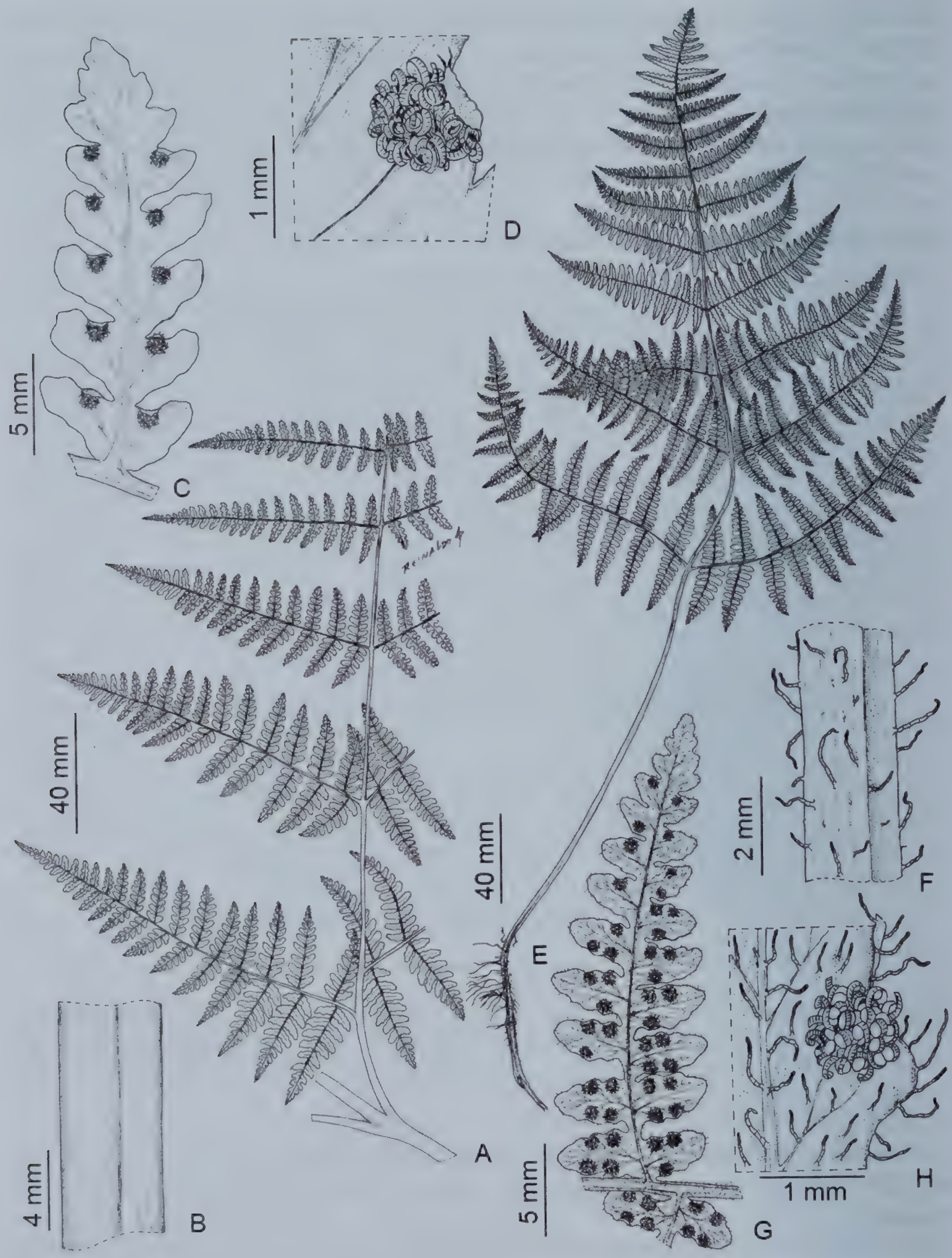

FIG. 3. A–D *Hypolepis miodelii* (*Brade 16418*). A. Basal pinna (part of the basicopic side removed). B. Petiole. C. Segment, abaxially. D. Detail of sorus and indusium. E–H. *Hypolepis sundei* (*van der Werff 25054*). E. Habit. F. Petiole, showing catenate-glandular hairs. G. Pinnule, abaxially. H. Detail of sorus, indusium, and laminar margins.

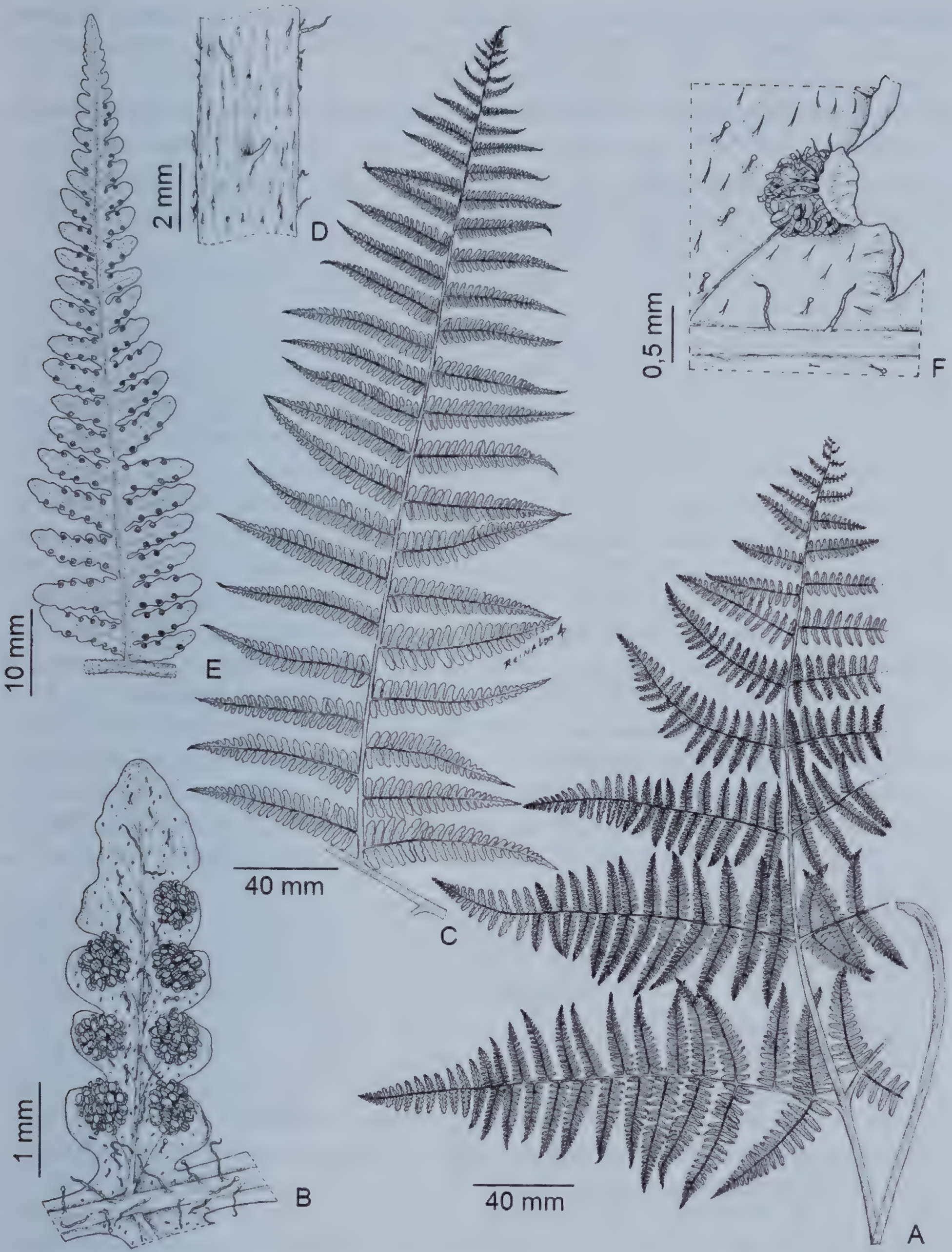

FIG. 4. A–B *Hypolepis rigescens* var. *paranaensis* (*Dusén 10222*). A. Leaf (the proximal pinnae were lowered). B. Segment, abaxially. C–F *Hypolepis stuebelii* (*Smith 2847*). C. Medial pinna. D. Petiole, showing aculei and hairs. E. Pinnule, abaxially. F. Detail of sorus, indusium, and laminar tissue between the veins with acicular and glandular hairs.

rugose, abaxially and adaxially tomentose; *basal pinnae* ca. 35–50 × 15–40 cm, inequilateral; *costae* abaxially tomentose, adaxially sparsely strigose, the *hairs* longer than those on petioles and rachises, 10–15-celled, 0.7–1 mm long; *costules* abaxially tomentose, adaxially sparsely hairy; *veins* abaxially tomentose, adaxially sparsely hairy; *laminar tissue between the veins* abaxially tomentose, (the lamina surface not visible), adaxially glabrous; *laminar margins* glabrous; *sori* abaxial-marginal; *indusia* reflexed, yellowish hyaline, the margins glabrous or with a few hairs.

Distribution and ecology.—Costa Rica, Colombia, Ecuador, and Peru; from 3000 to 3500 m.

Etymology.—The specific epithet honors Dr. Brigitte Zimmer (1943–), senior researcher and curator of ferns at Botanischer Garten und Botanisches Museum Berlin-Dahlem (B). Zimmer has made many contributions to Pteridology, especially at the nomenclature section of the International Botanical Congresses and in the taxonomy of the genus *Adiantum*.

Specimens examined.—COSTA RICA. **Cartago:** Vicinity of Millsville, Pan American highway, about 3 km above Nivel, 3000–3300 m, 22 Jul 1949, *R.W. Holm & H.H. Iltis 501* (BM); Cerro de la Muerte, west of Pan American Highway, near km 90, 11,500 ft, 9 Aug 1967, *A.M. Evans & F. Bowers 3212* (VT-on 2 sheets); Cerro de la Muerte, south of peaks, 2800 m, 27 Dec 1970, *D.S. Barrington 354* (VT-on 7 sheets); Cerro de la Muerte, on road to San Isidro del General, 3100 m, 12 Feb 1980, *H. Churchill 3488* (VT-on 3 sheets).

COLOMBIA. **Cundinamarca:** Guadalupe, 5 east of Bogotá, 10,900 ft, 1 Jan 1945, *E.L. Little et al. 9189* (GH).

ECUADOR. **Carchi:** Montufar Cantón, 00°35′05″N, 77°42′00″W, 3500 m, *A. Fay & L. Fay 4336* (MO-*n.v.*, NY). **Loja:** East of Yangana, Cerro Toledo, Parque Nac. Podocarpus, 04°24′S, 79°06′W, 3300–3450 m, 23 Feb 1985, *B. Øllgaard et al. 58020* (AAU-*n.v.*, NY).

PERU. **Amazonas:** along road Jumbilla – Rodriguez de Mendonza, 06°07′29″S, 77°38′51″W, 3000–3400 m, 10 Nov 2012, *H. van der Werff et al. 25433* (MO-*n.v.*, UC). **Department unknown:** Reise von Pacaomayo – Mogobamba, Bogazan, 3000 m, s.d., *A. Stübel 1071* (B).

Hypolepis zimmerae is easily recognized by the intermittent growth pattern of leaves, and densely tomentose petioles, laminar axes, and abaxial surface of blades that are fully covered by long, lax, catenate-acicular hairs (Figs. 1A–D). The intermittent leaves and high elevation habitat suggest that *H. zimmerae* forms a natural group along with *H. flexuosa* Sodiro, *H. muenchii* (Christ) Mickel, and *H. thysanochalena* Mickel & Beitel. *Hypolepis zimmerae* co-occurs with *H. flexuosa* in Peru, Colombia, and Costa Rica, while *H. muenchii* and *H. thysanochalena* are restricted to Mexico.

Schwartsburd (2012) had segregated *H. zimmerae* from *H. flexuosa,* as *Hypolepis flexuosa* var. *zimmerae* Schwartsb. & J. Prado, but this name was never validly published as it only appeared in a PhD dissertation (Art. 30.9 of the Code—Turland *et al.*, 2018). *Hypolepis zimmerae* differs from *H. flexuosa* by shorter leaves, to 2 m long (*vs.* to 6 m long), and densely tomentose petioles, laminar axes, and abaxial blade surfaces (*vs.* sparsely lanose to glabrescent) (Figs. 1A–D).

Hypolepis flexuosa Sodiro (see Figs. 8A, B, D–G in Schwartsburd and Prado, 2015, on page 275).

Plants terrestrial. *Rhizomes* 4–10 mm diam.; *the hairs* catenate-acicular, yellowish brown, 0.3–0.6(–1) mm long, 6–12(–15)-celled. *Leaves* intermittent, scandent, (1–)2–6 m long; *petioles* (0.5–)1–3 m × (4–)7–15 mm, proximally purplish, distally light reddish-brown, inermous, rugose, glabrescent, the *hairs* catenate-acicular, lax, 0.2–0.4 mm long, 4–8-celled; *blades* proximally quadripinnate-pinnatifid to pentapinnate, (0.5–)1–3 × (0.6–)1–3 m; *rachises* flexuous, proximally light reddish-brown, stramineous above, inermous, rugose, glabrescent; *basal pinnae* (30–)50–150 × (20–)40–70 cm, inequilateral; *costae* abaxially lanose, adaxially glabrescent, the *hairs* longer than those on the petioles, 0.3–1 mm, 6–15-celled; *costules* abaxially sparsely lanose to glabrescent, adaxially glabrescent; *veins* abaxially sparsely lanose to glabrescent, adaxially glabrescent; *laminar tissue between the veins* abaxially sparsely lanose to glabrescent, adaxially glabrous; *lamina margins* glabrous; *sori* abaxial-marginal; *indusia* proximally greenish, distally hyaline, the margins crenate, dentate, glabrous or rarely with two or three hairs.

Distribution and ecology.—Costa Rica, Colombia, Ecuador, Peru, and Bolivia; from 2000 to 4050 m.

Hypolepis sunduei Schwartsb., ***sp. nov.*** TYPE.—PERU. **Amazonas:** Along road to Tialango, 05°52′31″S, 76°46′36″W, 2100 m, 4 Nov 2012, *H. van der Werff, L. Valenzuela, G. Shareva & A.R. Barrantes 25054* (holotype: UC!; isotype: MO-*n.v.*). **Figs. 3E–H.**

Diagnosis.—Inermous petioles and rachises, blades copiously furnished with only catenate-glandular hairs throughout, and glandular-hairy laminar margins. Differs from *Hypolepis viscosa* by much longer catenate-glandular hairs on the lamina margins, to 0.8 mm long.

Plants terrestrial. *Rhizomes* 3–4 mm diam.; *the hairs* catenate-acicular, yellowish brown, 2–3 mm long, 15–20-celled. *Leaves* determinate, erect, 35–40 cm long; *petioles* 10–20 cm × 1.5–2.5 mm, light brown, inermous, rugose, densely villous, the *hairs* catenate-glandular 6–12-celled, 0.4–0.8 mm long, and with scattered hairs similar to those on the rhizomes; *blades* proximally tripinnate-pinnatifid, 25–30 × 25–30 cm, herbaceous; *rachises* straight or slightly flexuous, light brown, inermous, rugose, densely villous, with hairs similar to those on the petioles; *basal pinnae* 12–15 × 5–7 cm, equilateral; *costae* abaxially and adaxially densely villous, with only catenate-glandular hairs similar to those on the petioles and rachises; *costules* abaxially and adaxially villous, with catenate-glandular hairs; *veins* abaxially and adaxially villous, with catenate-glandular hairs; *laminar tissue between the veins* abaxially and adaxially villous with catenate-glandular hairs; *laminar margins* copiously hairy with catenate-glandular hairs; *sori* abaxial-marginal;

indusia slightly reflexed, minute, slightly differentiated, with glandular-hairy margins.

Distribution and ecology.—Known only from the type collection; probably endemic to northern Peru; from 2100 m.

Etymology.—The specific epithet honors Dr. Michael A. Sundue (1975–), research assistant professor in the Plant Biology Department and curator at the Pringle Herbarium at the University of Vermont. Sundue is an active researcher specializing in the taxonomy, phylogeny, and evolution of ferns, especially the Grammitids.

Hypolepis sunduei resembles *H. viscosa* H. Karst., which occurs in Hispaniola, Colombia, and Venezuela, in the inermous petioles and rachises, the blades copiously furnished with catenate-glandular hairs throughout, and glandular-hairy laminar margins. Besides geographical distribution, *H. sunduei* differs from *H. viscosa* by having shorter leaves, to 40 cm long (*vs.* to 2 m), only catenate-glandular hairs on rachises and costae (*vs.* catenate-acicular and catenate-glandular hairs present), and much longer catenate-glandular hairs on the lamina margins, to 0.8 mm long (*vs.* to 0.2 mm) (Figs. 3E–H).

Hypolepis sunduei resembles *H. minima* M. Kessler & A.R. Sm., which is endemic to Bolivia, by the small size of its leaves. *Hypolepis sunduei* also differs from *H. minima* by having only catenate-glandular hairs on the rachises and costae (*vs.* both catenate-acicular and catenate-glandular hairs), and by the copiously glandular-hairy laminar margins (*vs.* glabrous laminar margins) (Figs. 3E–H).

New taxa from the Brazilian Guiana Highlands and from the Brazilian Atlantic Forest

Hypolepis forzzae Schwartsb., ***spec. nov.*** TYPE.—BRAZIL. **Amazonas:** Santa Isabel do Rio Negro, Parque Nacional do Pico da Neblina, trilha da Bacia do Gelo para Serra do Vento, 0°47′14″N, 66°01′26″W, 2000 m, 22 Sep 2012, *R.C. Forzza 7277, G. Martinelli, D.P. Costa, M.A. Moraes, M.A. Nadruz & M.R. Blind* (holotype: RB!-on 4 sheets; isotype: VIC!). **Figs. 2E–H.**

Diagnosis.—Similar to *Hypolepis repens,* but with sparsely aculeate, reddish brown petioles and rachises, and slightly reflexed, minute indusia.

Plants terrestrial. *Rhizomes* 5–7 mm diam.; *the hairs* catenate-acicular, yellowish brown, 2–3 mm long, 20–30-celled. *Leaves* determinate, arched, ca. 1.7 m long; *petioles* 70–80 cm × 5–8 mm, proximally dark brown, distally reddish brown, essentially glabrous but with trichomidia restricted to the adaxial groove, rugose, sparsely aculeate, the *aculei* sparse, straight, 0.2–0.7 mm long; *blades* proximally quadripinnate-pinnatifid, ca. 1.2 × 1.2 m, herbaceous; *rachises* straight, reddish brown, sparsely aculeate, non-rugose, with trichomidia restricted to the adaxial groove; *basal pinnae* ca. 60 × 40 cm, inequilateral; *costae* abaxially sparsely pilose, adaxially densely pilose, the *hairs* catenate-acicular, 4–10-celled, 0.3–0.7 mm long; *costules* abaxially sparsely pilose, adaxially pilose; *veins* abaxially glabrescent, adaxially sparsely pilose; *laminar tissue between the veins* abaxially and adaxially glabrous; *laminar margins* glabrous; *sori* abaxial-marginal; *indusia* slightly reflexed, minute, partly covering the sori, hyaline, the *margins* glabrous or rarely with 1–2 hairs.

Distribution and ecology.—Known only from the type collection; probably endemic to the Neblina group of tepuis, in the border of Brazil (state of Amazonas) and Venezuela (state of Amazonas); from ca. 2000 m.

Etymology.—The specific epithet honors Dr. Rafaela Campostrini Forzza (1972–), researcher and herbarium curator of Jardim Botânico do Rio de Janeiro (RB). Forzza is an active plant collector and taxonomist specializing in the Bromeliaceae. She is the senior collector of the type of *Hypolepis forzzae,* during the project entitled "Montanhas da Amazônia" (see Barbosa-Silva *et al.* 2016).

Hypolepis forzzae is characterized by reddish brown petioles and rachises that are sparsely armed with aculei; sparsely pilose costae, costules, and veins, furnished with catenate-acicular hairs; and slightly reflexed, minute indusia partly covering the sori (Figs. 2E–H). It differs from *H. repens* by the reddish brown petioles and rachises (*vs.* proximally dark brown, distally light brown to stramineous), which are sparsely aculeate (*vs.* densely aculeate); the aculei to 0.7 mm long (*vs.* to 4 mm); and slightly reflexed, minute indusia partly covering the sori (*vs.* reflexed indusia completely covering the sori).

Hypolepis miodelii Schwartsb., ***spec. nov.*** TYPE.—BRAZIL. **Rio de Janeiro:** [Teresópolis], Serra dos Órgãos, Pedra do Frade, 1400 m, 19 Jul 1940, *A.C. Brade 16418* (holotype: RB!-on 3 sheets; isotypes: CESJ!-3128, K-*n.v.,* MBM-*n.v.,* NY-*n.v.,* SP!, VIC!-frag.). **Figs. 3A–D.**

Diagnosis.—Inermous petioles and rachises; abaxially glabrous costae, costules, veins, and laminar tissue between the veins; slightly reflexed, minute indusia that partly cover the sori, with hairy margins.

Plants terrestrial. *Rhizomes* 3.5–5 mm diam.; *the hairs* catenate-acicular, yellowish brown, 1.5–3 mm long, 15–30-celled. *Leaves* determinate, arched, ca. 1–1.5 m long; *petioles* 60–70 cm × 4–6 mm, lustrous dark brown, inermous, non-rugose, glabrous; *blades* proximally quadripinnate-pinnatifid, ca. 1 × 1 m, herbaceous; *rachises* straight, proximally lustrous dark brown, distally light brown, inermous, non-rugose, essentially glabrous (trichomidia restricted to the adaxial groove); *basal pinnae* ca. 45–50 × 30–35 cm, subequilateral; *costae* abaxially glabrous, adaxially with scattered catenate-acicular hairs, 0.4–0.5 mm, 5–6-celled; *costules* abaxially and adaxially glabrous; *veins* abaxially and adaxially glabrous; *laminar tissue between the veins* abaxially and adaxially glabrous; *laminar margins* glabrous; *sori* abaxial-marginal; *indusia* slightly reflexed, minute, partly covering the sori, yellowish, the *margins* copiously hairy.

Distribution and ecology.—Known only from the type locality; probably endemic to *Serra dos Órgãos,* in the state of Rio de Janeiro, Brazil; from ca. 1400–1700 m.

Etymology.—The specific epithet honors Dr. Miodeli Nogueira Jr. (1981–), assistant professor and researcher at Universidade Federal da Paraíba. Miodeli is an active researcher specializing in the ecology and taxonomy of marine plankton. He has also helped me greatly during the field trips to collect ferns for my Master Thesis, from 2003 to 2006, and for my Doctoral Dissertation, in 2010, including some type specimens (see specimens listed in Schwartsburd and Labiak 2007, for example).

Specimens examined.—BRAZIL. **Rio de Janeiro:** Theresópolis, Toca dos Caçadores, 1400–1700 m, 19 Sep 1929, *A.C. Brade 9294* (R-on 2 sheets); Theresópolis, Pedra do Frade, 1400 m, 26 Sep 1929, *A.C. Brade s.n.* (R-21046 [on 2 sheets]); Theresópolis, Guarany, 1500 m, 4 Oct 1929, *A.C. Brade 9579* (R).

Hypolepis miodelii has essentially glabrous leaves, apart from a few trichomidia restricted to the adaxial groove of rachises and scattered catenate-acicular hairs adaxially on pinna-rachises and costae. This minimal indument is unique among the Brazilian Atlantic Rain Forest species of *Hypolepis*. All others have catenate-acicular and/or catenate-glandular hairs on both sides of rachises, pinna-rachises, costae, costules, and veins. *Hypolepis miodelii* is also characterized by inermous and non-rugose petioles and rachises that are lustrous dark brown, and slightly reflexed, minute, hairy indusia that partly cover the sori (Figs. 3A–D).

Hypolepis miodelii, with its essentially glabrous leaves, is morphologically more similar to species of the *Hypolepis nuda*-complex (*H. eckmanii* Maxon, *H. nuda* Mett., *H. trichobacilliformis* R.C. Moran, and *H. urbanii* Brause) from northern South America and Central America, rather than to the eastern Brazilian species. Apart from the geographical distribution, *Hypolepis miodelii* differs from all of them by not having bacilliform trichomidia, which are found copiously on the laminar axes of those species.

Hypolepis rigescens var. ***paranaensis*** Schwartsb., ***var. nov.*** TYPE.—BRAZIL. **Paraná:** Alexandra, in cultis, 5 Sep 1910, *P.K.H. Dusén 10222* (holotype K!; isotypes: BM!, BR!, G!, GH!-00934323, GH!-00934323, LE!, NY!). **Figs. 4A, B.**

Diagnosis.—Differs from *Hypolepis rigescens* (Kunze) T. Moore var. *rigescens* by its dwarf size, shorter, erect leaves, more stout petioles, and ascendant pinnae.

Plants terrestrial. *Rhizomes* ca. 3 mm diam.; *the hairs* catenate-acicular, reddish-brown, 1–2 mm long, 15–20 celled. *Leaves* determinate, erect, 50–70 cm long; *petioles* 15–45 cm × 3–4 mm, proximally purplish, distally golden-brown, aculeate, rugose, abaxially and adaxially sparsely pilose to glabrescent, the *aculei* straight, to 1 mm long, the *hairs* of two kinds, the *first kind of hair* catenate-acicular, 0.1–0.2 mm long, 4–7-celled, the *second kind of hair* catenate-glandular, 0.1–0.5 mm long, 4–8-celled; *blades* ovate, proximally tripinnate-pinnatifid to quadripinnate, 30–40 × 40–70 cm, herbaceous to chartaceous; *rachises* straight, proximally golden-brown, distally stramineous, rugose, aculeate, abaxially and adaxially sparsely pilose, with hairs similar to those on the petioles; *basal pinnae* 20–35 × 12–17 cm, subequilateral; *costae* abaxially and adaxially densely pilose, with both kinds of hairs, but the first kind longer, 0.4–1.5 mm long, 7–15-celled; *costules* abaxially densely pilose, adaxially glabrescent, the hairs similar to those on costae; *veins* abaxially pilose, adaxially glabrescent, with only the second kind of hair, and this shorter, 0.1–0.15 mm long, 2–3-celled; *laminar tissue between the veins* abaxially with hairs similar to those on veins, adaxially glabrous; *lamina margins* glabrous; *sori* abaxial-marginal; *indusia* reflexed, proximally greenish, distally hyaline, the margins crenate to dentate, rarely with one or two hairs.

Distribution and ecology.—Known only from the type collection; probably endemic to the coastal region of the state of Paraná, Brazil; from ca. 200 m.

Etymology.—The varietal epithet represents the distribution of the taxon, which is endemic to the state of Paraná, in Brazil.

Hypolepis rigescens is a widespread species, occurring from Costa Rica to southern Brazil and Bolivia, and also in a wide range of elevation, from 400 to 2000 m (Schwartsburd and Prado 2016). Throughout most of its range, *H. rigescens* have leaves ranging from 1 to 2.3 m long, 0.5–0.8 m wide, and copiously aculeate petioles and rachises. Some specimens from Bolivia, have shorter leaves (0.3–1 × 0.2–0.5 m) and sparsely aculeate petioles and rachises. Schwartsburd *et al.* (2017) regarded these specimens as a local endemic variety, *H. rigescens* var. *buchtienii* (Rosenst.) Schwartsb. In the state of Paraná, southern Brazil, the specimens of *Hypolepis rigescens* are also different—they are dwarf sized with more stout petioles, and with ascendant pinnae. These specimens come from the southernmost limits of the species. Thus, I here describe this taxon as a new local endemic variety: *H. rigescens* var. *paranaensis*.

Hypolepis rigescens var. *paranaensis* differs from *H. rigescens* var. *rigescens* by its shorter, erect leaves, which are 0.5–0.7 × 0.4–0.7 m (*vs.* erect to arched leaves, 1–2.3 × 0.5–0.8 m), shorter and more stout petioles, 15–45 cm × 3–4 mm (*vs.* 40–100 cm × 2.5–6 mm), ascendant pinnae (*vs.* patent), and more densely pilose laminar axes (Figs. 4A, B).

Although also having short leaves, *Hypolepis rigescens* var. *paranaensis* differs from *H. rigescens* var. *buchtienii* by the more stout petioles, 3–4 mm diam. (*vs.* 1.5–2 mm), which are moderately aculeate (*vs.* sparsely aculeate), and by having only two kinds of hairs through the laminar axes (*vs.* three kinds of hairs; some unique long, reddish catenate-acicular hairs).

Hypolepis rigescens var. *paranaensis* is extremely rare or possibly extinct in nature, due to the historical deforestation of the Brazilian Atlantic Forest. The only herbarium specimens seen are collections made by Perl Karl H. Dusén, in the early 20th century. There are no recent collections in the local herbaria (*e.g.*, MBM, UPCB), and the locality cited by Dusén has been relatively well sampled by contemporary botanists.

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The Articulated and Non-Articulated Stem in *Selaginella* (Selaginellaceae - Lycopodiopsida)

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Abstract.—The present investigation presents a clear differentiation between the articulated and non-articulated stem of *Selaginella*, based on morphological and anatomical characteristics. We also take the first step in developing a clear definition of the articulated stem in *Selaginella*. Further, in *Selaginella anaclasta* previously described as having articulate stems, we found no micro-morphological or structural evidence of articulations, and we describe this species as one with non-articulated stems. In support of our findings, we present micromorphological and structural descriptions of three species *S. anaclasta*, *S. exaltata*, and *S. parviarticulata*, which differentiate the various stem constructions in *Selaginella*.

Key Words.—anatomy; Brazilian Amazonia; Lycophytes; spikemoss; taxonomy.

Selaginella anaclasta Alston ex Crabbe & Jermy, a spikemoss species known from very few collections, occurs in Venezuela and Brazil (Smith, 1995; Barbosa-Silva *et al.*, 2016). Crabbe and Jermy (1973), Somers (1978), Smith (1995) and Assis (2016) described *S. anaclasta* as a species having articulate stems, whereas Góes-Neto (2016) allied *S. anaclasta* with species lacking articulate stems. Nonetheless, features common to other "articulate" group species were present in *S. anaclasta*, e.g., each strobilus had only a single (rarely two) basal megasporangium, megasporophylls were ca. two times longer than microsporophylls, the reticulate ornamentation on megaspores contained high muri, and rhizophores arose dorsally from stems (Spring, 1849; Hieronymus and Sadebeck, 1901; Walton and Alston, 1938; Somers, 1978; Somers, 1982).

Articulations in *Selaginella* P. Beauv. species usually occur just beneath branching, forming a swelling or a dark band, which is best seen on dry specimens (Somers, 1978). Articulations are easily observed on main stems but are often distinct on branches as well. Species with articulations were traditionally treated within *Selaginella* [unranked] *Articulatae* Spring (Spring, 1849; Braun, 1865; Hieronymus and Sadebeck, 1901; Walton and Alston, 1938; Jermy, 1986; Zhou *et al.*, 2016). Species having articulations were commonly recognized as a separate group (e.g., Spring, 1849; Braun, 1865; Hieronymus and Sadebeck, 1901; Walton and Alston, 1938; Jermy, 1986; Zhou *et al.*, 2016). Most recently, Weststrand and Korall (2016) recognized two closely related subgenera such as *Selaginella* subg. *Gymnogynum* (Beauvois) Weststrand & Korall, in which all species are described with articulations, and *Selaginella* subg. *Exaltatae* Weststrand & Korall, which included some species with articulate stems and some lacking this feature.

Following Somer's description in 1978, other types of articulation were described, some with an imprecise characterization such as "inconspicuous type" (Assis, 2016). In general, classifications based on articulations lack a clear definition of this character (Crabbe and Jermy, 1973; Somers, 1978; Smith, 1995; Assis, 2016; Góes-Neto, 2016), including its anatomy, function, and consequently its importance to the systematics of *Selaginella*. The aim of this study was to explore whether *Selaginella anaclasta* has articulate stems, and to compare the articulate structure of *S. anaclasta* with two other articulate Brazilian species *S. exaltata* (Kunze) Spring and *S. parviarticulata* Buck.

Materials and Methods

Taxon sampling.—In order to verify the presence or absence of articulations in the stems of *S. anaclasta*, two other Brazilian species (*S. exaltata*, with conspicuous articulations, and *S. parviarticulata*, with inconspicuous articulations) were chosen for comparison. The present analysis was based on observation of specimens of *S. anaclasta* (P. H. Labiak *et al.* 5639, RB), *S. exaltata* (T. E. Almeida & A. Salino 2557, BHCB), and *S. parviarticulata* (R. Viveros 251, BHCB), as well as high resolution scanned images of the holotype of *S. anaclasta* available at the US herbarium website (http://plants.jstor.org/; US00433013). Herbarium acronyms follow *Index Herbariorum* of Thiers (2017, continuously updated).

Three to four samples of the stem of each species with branch bifurcations were observed via stereo-microscope (avoiding removal of the microphylls), light microscope, and scanning electron microscope. In addition, the stem anatomy of these species was observed and compared.

Light microscopic and stereomicroscopic examination.—Stem materials from herbarium specimens were rehydrated (Smith and Smith, 1942) and stored in 70% ethanol. Subsequently, the fragments were dehydrated in decreasing ethanol series and embedded in 2-hydroxyethyl methacrylate resin for sectioning (Historesin Leica, solutions prepared according to manufacturer's instructions), following Meira and Martins (2003). All samples were longitudinally sectioned at a thickness of 3 to 4 μm using a rotary microtome (Leica Biosystems RM2245). Sections were stained with toluidine blue at pH 4.6 (O'Brien, Feder, and McCully, 1965) and slides were mounted in resin. Observations and photographic documentation were performed using a stereomicroscope (Carl Zeiss Discovery V8) equipped with a digital camera (Carl Zeiss AxioCam ICc5).

Scanning electron microscopic examination.—Samples were transferred from herbarium specimens to aluminum SEM stubs coated with double-sided carbon tape, and then coated with gold using a FDU 010 sputter coater (Bal-

Tec, Balzers, Liechtenstein). Examination of specimens and image capture were conducted using a scanning electron microscope FEI Quanta 200F (FEI Company, ETH Zürich), with an accelerating voltage of 15 kV, in the Center for Microscopy at the Universidade Federal de Minas Gerais.

Results

According to the observation and study, the stem can be divided into two regions *viz.* the articulate region (just below the stem bifurcation) and the non-articulate region (the rest of the stem below the articulation up to the stem bifurcation).

Longitudinal sections were useful in observing anatomical characteristics of the stem. The articulate region in *S. exaltata* is characterized by a pectic unistratified epidermis and subjacent layers of cortex, consisting of thin, elongate cells that occurred along the longitudinal axis and had predominantly pectic cell walls, (Figs. 1A-C). In the articulate region, stems have two evident constrictions, which affect both the epidermis and the first subjacent cortical layer (Figs. 1B-C). The non-articulate region was composed by cells with thickened and cellulosic cell walls (Fig. 1B).

The articulate region of *S. parviarticulata* has a slight increase in the number of cortical cells relative to those in the non-articulate region, without differences in the chemical constitution of the cell wall (Figs. 1D-F). In contrast, *S. anaclasta* contains epidermis and cortex with tabular cells and thin cell walls. Both in the articulate and non-articulate region there is no structural distinction throughout the stem (Figs. 1G-I), *i.e.*, there are no constrictions or any modification in the number of cells or in the characteristics of the cell wall as observed in the other species analyzed. The main features among the species are summarized in Table 1.

Discussion

Based on our observations, the differences in the stems in these articulate species can be summarized by changes of the cell wall composition and constrictions and/or hyperplasia in the articulate region. Stable classification of morphological structures usually requires anatomical characterization. Descriptions based solely on morphology are often not sufficient to judge the role and importance of the plant structure (Lersten and Curtis, 1996).

According to Hieronymus and Sadebeck (1901) the articulations serve as a means of vegetative reproduction, because the stem can be broken at the articulate region and then transported to new sites where they may develop. However, based on current knowledge, the theory of Hieronymus and Sadebeck cannot be verified. Alternatively, while conferring resistance and protection to the cells, articulate regions may be characterized by primary cell walls with greater flexibility and permeability than non-articulate regions. It is possible that the presence of articulations is more directly related to the flexibility of stems, especially in species with scandent and erect habits that

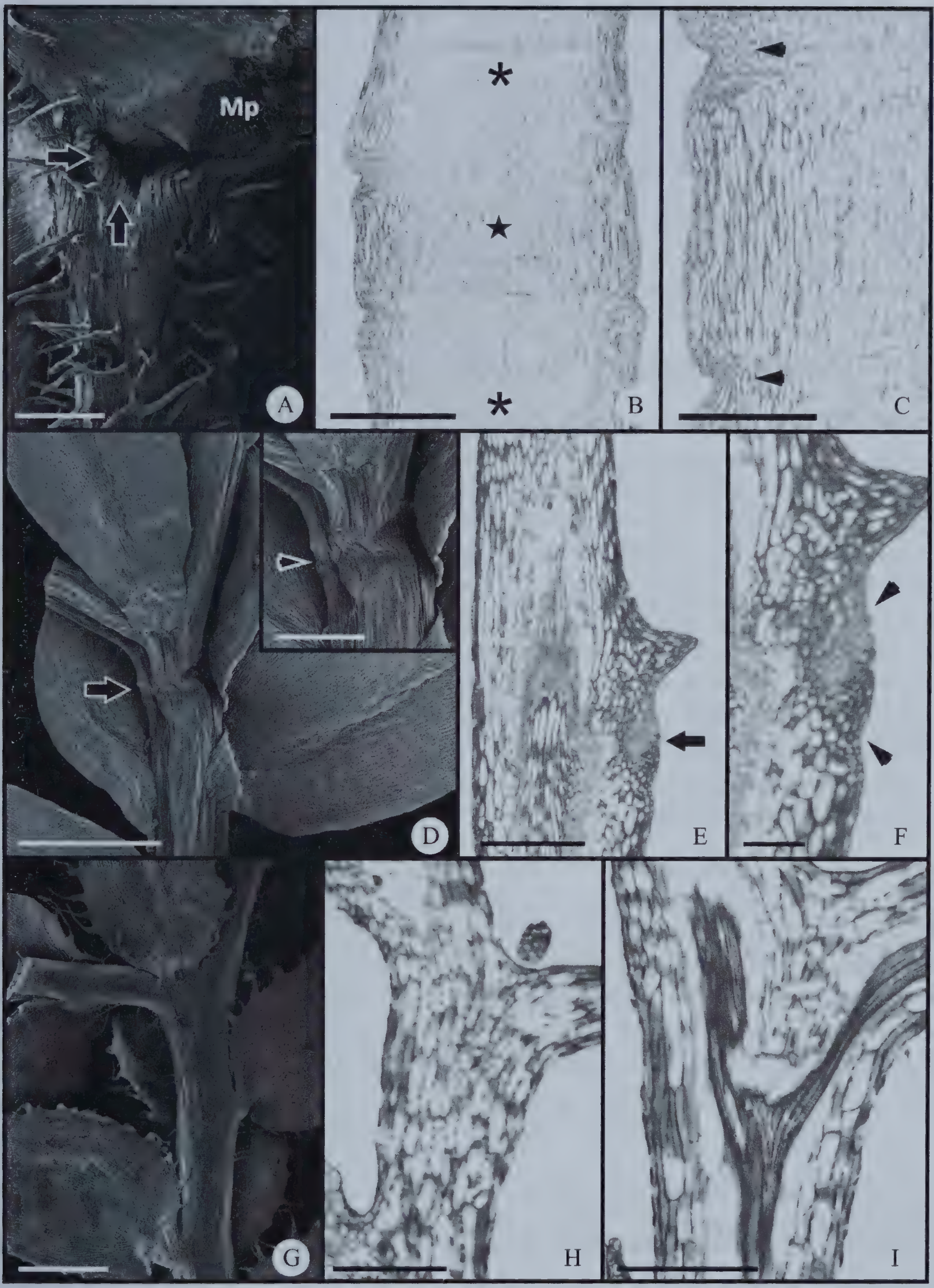

FIG. 1. A-C. Stem of *Selaginella exaltata* (T. E. Almeida & A. Salino 2557, BHCB). **A**. The articulate region (arrows) with one dorsal microphyll removed (Mp). **B**. The articulate region (star) and non-articulate region (asterisks). **C**. Two conspicuous constrictions delimiting the articulation; note the constrictions in detail (arrowhead). **D-F**. Stem of *Selaginella parviarticulata* (R. Viveros 251, BHCB). **D**. showing the frontal view of the articulate region (arrowhead), **E**. the anatomy of the

Table 1. Morfoanatomical characteristics of the articulations in the *Selaginella* species

	Species		
Stem region	*S. exaltata*	*S. parviarticulata*	*S. anaclasta*
articulate region	two evident constrictions, pectic cell wall	increase in the number of cells	-
non-articulate region	cells with thickened and cellulosic cell walls	-	-

Note: (-) without constrictions or any modification in the number of cells or in the characteristics of the cell wall as observed in the other species analyzed.

are more susceptible to abiotic factors such as wind, rain, and physical impacts.

Regarding the absence of morphological and anatomical modification in the region of the stem bifurcation in *S. anaclasta*, it is possible that the authors who first described *S. anaclasta* (Crabbe and Jermy, 1973) concluded that it was a species with articulate stems because it contained a set of features that allied it with other species traditionally treated as "*Articulatae*" (Spring, 1849; Braun, 1865; Hieronymus and Sadebeck, 1901; Walton and Alston, 1938; Jermy, 1986; Zhou *et al.*, 2016; Weststrand and Korall, 2016). These features included strobili with a single (rarely two) basal megasporangium, megasporophylls *ca.* twice as long as microsporophylls, megaspores having reticulate ornamentation, and rhizophores arising from the dorsal side of stems. However, based on our observations, *S. anaclasta* is a species without articulate stems.

Conclusions

As an important diagnostic characteristic, articulations in *Selaginella* still lack a clear structural definition. In the present study, we provide new information on articulations, which is a first step to defining this feature. Further studies with more sampling of *Selaginella* species, associating anatomy and phylogenetic data, may help to understand how important this character is in *Selaginella* and its evolutionary history.

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modified region just below stem bifurcation (arrow), **F** Detail showing the increase in the number of cells in articulate region (arrowhead). **G-I**. Stem of *Selaginella anaclasta* (P. H. Labiak *et al.*, 5639, RB). **G.** Lower surface of stem with absence of articulation, **H.** Region just below stem bifurcation, showing both the paradermic section and more internally in **I**, the region of the vascular system. Bars: 1 mm (B), 500 μm (D, G), 400 μm (C), 300 μm (A, E, H), 200 μm (I, inset D), 100 μm (F).

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SHORTER NOTE

An Ornamental Plant Found Spreading Aggressively: Potential Invasiveness of *Dryopteris erythrosora* (Dryopteridaceae) in North America.—*Dryopteris erythrosora* (D.C. Eaton) Kunze (Dryopteridaceae) is a fern native to Japan, Korea, and China (Hoshizaki and Wilson, American Fern Journal 89:1–98. 1999). It is valued for its striking coppery new growth, its hardiness, shade tolerance, and its evergreen habit. It has been widely planted in North America as an ornamental fern, frequently in large commercial landscape plantings. *Dryopteris erythrosora* is widely sold at garden centers and is frequently recommended by gardeners and even botanical gardens as a maintenance-free, easy-to-grow fern. In the summer of 2017 one of the authors noticed a dense population of *D. erythrosora* in a disturbed suburban woodlot, located in Alpharetta, Georgia. A population survey at the site documented a large number of fertile leaves and the recruitment of young plants.

There are increasing numbers of reports of this species naturalizing in the southeastern United States. Two occurrences of *D. erythrosora* outside of cultivation in Georgia were entered in to the Early Detection & Distribution Mapping System, an invasive species distribution map, by Jane Trentin (Bargeron, et al., EDDMAPS 2017). The first author visited one of these sites and observed numerous autumn ferns along creek banks on the Cherokee Trail at Stone Mountain Park. Autumn fern is beginning to spread in the same way through Fernbank Forest in Decatur, GA, and can be found on the banks of Lullwater Creek; a tributary of Peavine Creek in Atlanta, GA (Trentin, pers. comm. 2017). We have also been informed that *D. erythrosora* is naturalizing in several units of the Chattahoochee River National Recreation Area, north of Atlanta, Georgia (Hightower, pers. comm. 2017). Six recent collections have been made from three other Georgia counties in the Atlanta and Athens areas (Zomlefer, *et al.* Castanea 83:124-139, 2018). Beyond Georgia, a single plant is reported to have grown to eight leaves, four of which were fertile, and had persevered through at least two winters in Hot Spring County, Arkansas. The source of this plant is unknown, the closest potential source being 10 miles away (Simpson, *et al.*, American Fern Journal 98:111–112. 2008). *Dryopteris erythrosora* was also found growing in disturbed suburban woods, in Durham County, North Carolina; there was no indication that the ferns had been planted in the vicinity (Rothfels, *et al.*, American Fern Journal 102:184–186, 2012). However, it has been collected in several counties nearby and could have escaped from cultivation (SERNEC Data Portal, http//:sernecportal.org/portal/index.php, 2018). *Dryopteris erythrosora* has been included in the New Invaders of the Southeast field guide (Rawlins, *et al.*, 2018). Additional records of this taxon in North America are listed on Global Biodiversity Information Facility,

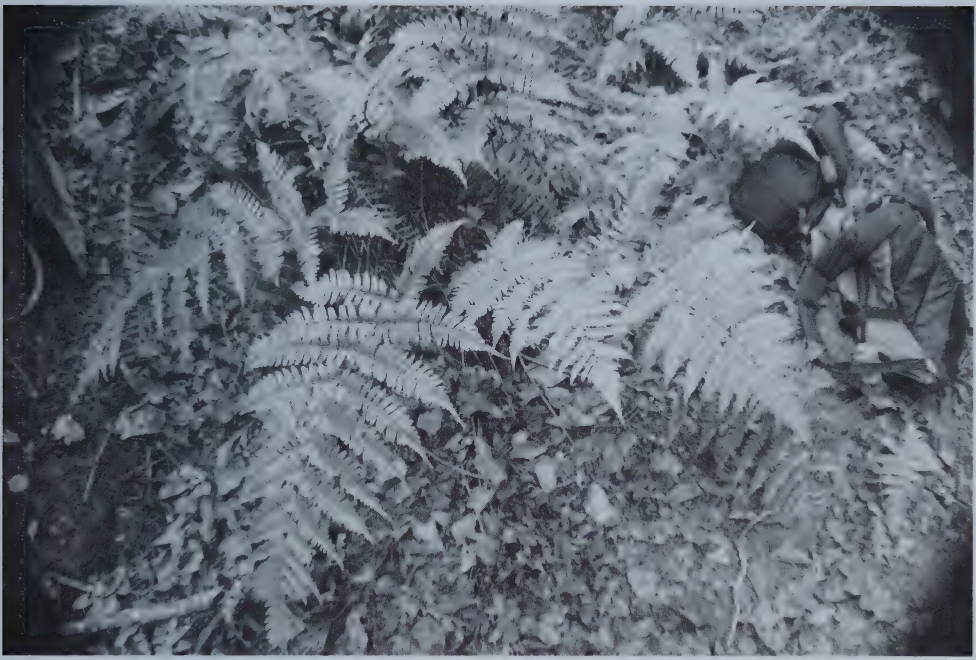

FIG. 1. Cluster of mature plants

especially near New York City and Washington D.C. (GBIF.org, https://doi.org/10.15468/dl.fpwlzt, 2018).

MATERIALS AND METHODS

During a plant identification course at the University of North Georgia, the first author of this paper discovered a large colony of *D. erythrosora* spreading aggressively down a moist embankment in Alpharetta, Georgia. The identification was by its five vascular bundles in the base of the petiole, deep red indusia-covered sori, and its abundant dark scales (Weakley, Flora of the Southern and Mid–Atlantic States, 2015). Other noteworthy characteristics of *D. erythrosora* are its triangular, bipinnate fronds that mature to a deep glossy green (Fig.1). On October 21, 2017 six undergraduate students surveyed the site, counting the numbers of plants present. Several vouchers were collected to support our research and will be kept in the University of Georgia Herbarium. A map of the distribution is provided to illustrate the extent of the invasion (Fig. 2).

RESULTS AND DISCUSSION

Six groups were counted, comprising 894 individuals, including young and adult sterile plants, as well as 337 sporulating individuals (Table 1); the population appeared to be robust and is likely spreading. Downhill from a

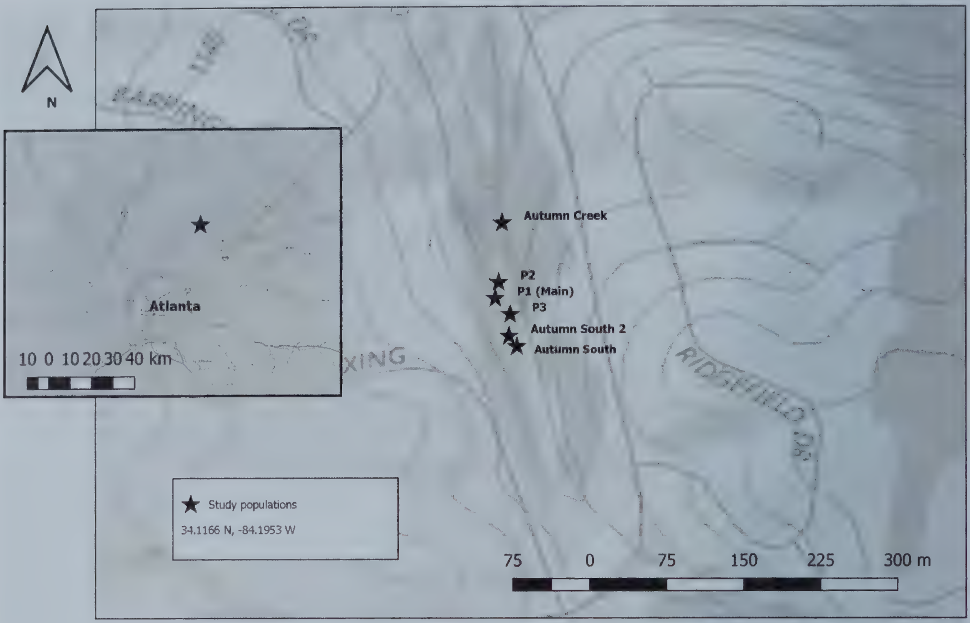

FIG. 2. Map of population

Pinus taeda tree line, the understory of this disturbed suburban woodlot also included *Ligustrum sinense, Vitis rotundifolia, Microstegium vimineum, Galium* sp., *Duchesnea indica, Youngia* sp., *Solanum carolinense, Phytolacca americana, Toxicodendron radicans, Stellaria* sp., *Rubus* sp., *Smilax* sp., *Parthenocissus quinquefolia,* and *Oxalis stricta.* Other ferns present were *Asplenium platyneuron, Onoclea sensibilis, Polystichum acrostichoides,* as well as another *Dryopteris* species. The plants at this site have not been removed, thus they can continue to be monitored for future study. To this point, *D. erythrosora* has not been considered invasive, but the data collected suggests that it is capable of self-replicating and maturing into well-established colonies in the wild similar to *Macrothelypteris torresiana,* another ornamental fern that is invasive to the southeastern United States (Leonard, American Fern Journal 62:97–99, 1972; Guertin and Tess, U.S. Army Corps of Engineers

TABLE 1. Stem count from population in Alpharetta, Georgia, October 2017

Population	Young plants (no sori)	Adult plants (no sori)	Adult plants (sori present)	Total
P1 (Main)	197	171	245	613
P2	35	76	69	180
P3	6	49	22	77
Autumn South	0	6	1	7
Autumn South2	0	4	0	4
Autumn Creek	0	13	0	13

ERDC/CERL TR-06-12, 2006). We plan to repeat the survey through time to measure the trend in population growth and evaluate the invasiveness of autumn fern. Once relative population invasiveness is assessed, we can recommend an appropriate management plan.

Acknowledgments

We thank The University of North Georgia Department of Biology for offering courses that make these discoveries possible, the undergraduate students who volunteered to help collect data, Brandon Fuller for photography, Jane Trentin and Jerry Hightower for guiding us in our exploration, and Karan Rawlins for granting us access to her publication. We also thank Weston Testo for his early review of this manuscript, and Dan Spaulding of the Anniston Natural History Museum (Anniston, AL) for his help confirming the ID of this fern.—H. Umstead and J.T. Diggs. 3820 Mundy Mill Rd, Oakwood, GA 30566. (HMUMST2401@ung.edu; Tom.Diggs@ung.edu)

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SHORTER NOTE

First Report of Foliar Nectar Production by *Lygodium microphyllum* (Lygodiaceae), an Invasive Fern in Florida.—Foliar nectar has been documented on 43 extant fern species belonging to nine genera in five families (Koptur *et al.*, Annals of Botany 111:1277–1283. 2013; Nepi *et al.*, Annals of Botany 104:205–219. 2009). Here we report the first observation of foliar nectar production by Old World climbing fern, *Lygodium microphyllum* (Cav.) R. Br., which is a member of a sixth family, Lygodiaceae.

The sole genus in the Lygodiaceae, *Lygodium*, comprises 40 species of climbing ferns with members native to southeast Asia, subtropical Africa, Australia, North and Central America, and northern South America (Kramer 1990, Schizaeaceae, 258–262 *in* The Families and Genera of Vascular Plants Vol. I. Pteridophytes and Gymnosperms, Springer-Verlag; Pemberton, American Fern Journal 88:176–182. 1998; Wikström, Kenrick, and Vogel, Review of Palaeobotany and Palynology 119:35–50. 2002). *Lygodium microphyllum* is the first species in the genus—indeed, in the order (Schizaeales)—for which foliar nectar has been reported. *Lygodium microphyllum* is native to tropical and subtropical areas of Asia, Africa, and Australasia (Pemberton, 1998). First cultivated in the USA as an ornamental, the species was reported as naturalized in Florida in 1965 (Beckner, American Fern Journal 58:93–94. 1968; Nauman and Austin, American Fern Journal 68:65–66. 1978). *Lygodium microphyllum* has since become widespread in wet and mesic environments of south and central Florida, infesting both natural areas and highly disturbed sites (Rodgers, Pernas, and Hill, Invasive Plant Science and Management 7:360–374. 2014). The invasive fern degrades habitats both by smothering native vegetation and by acting as a fire ladder, facilitating the spread of fire into tree canopies that would not normally burn (Pemberton and Ferriter, American Fern Journal 88:165–175. 1998; Schmitz et al. 1997, The Ecological Impact of Non-indigenous Plants. 29–74 *in* Strangers in Paradise, Island Press).

LYGODIUM MICROPHYLLUM PLANT ARCHITECTURE AND NECTAR PRODUCTION

For clarity, morphological descriptions follow terminology of Tryon (Taxon 9:104–109. 1960) and Vasco, Moran, and Ambrose (Plant Evolution and Development 4:1–13. 2013). The fronds of *L. microphyllum*, which are unusual in being indeterminate, are tripinnate, with alternating pinnae. Each pinna (Fig. 1) consists of a stalk (petiolule) with one set of opposite pinnules; the pinna terminates in a dormant pinna apex protected by numerous trichomes. Each pinnule has a secondary petiolule and is alternately divided into 4–13 tertiary segments. Each tertiary segment is also petiolulate. The pinnule-rachis refers to the midrib of the pinnule, including tertiary segment petiolules. Uniseriate trichomes are present on all surfaces but are especially abundant on the adaxial surface of the rachis, petiolules, and pinnule-rachis. Presence of

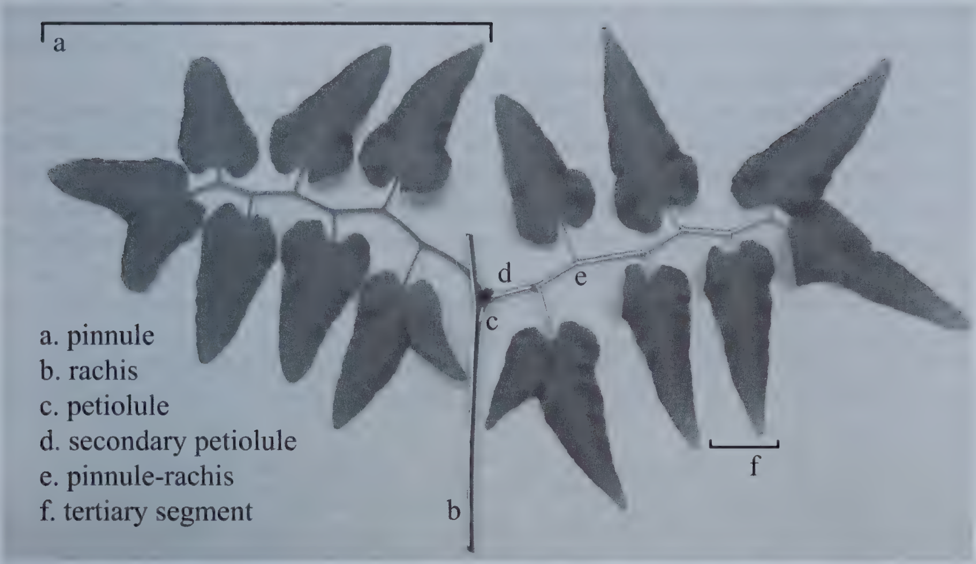

FIG. 1. Structure of a single pinna on the leaf of *Lygodium microphyllum*; pinnae alternate along the climbing, indeterminate leaf. Yellow and blue lines designate the rachis and parts of the pinna: long yellow (rachis, b), short blue (petiolule, c), short yellow (secondary petiolule, d), and long, branched blue (pinnule-rachis, e).

uniseriate hairs on the rachis has been previously reported in three genera of the order Schizaeales: *Schizaea*, *Anemia*, and *Lygodium* (Clarke, doctoral thesis U. Wisconsin. 1935)

Small beads of nectar were first observed in June 2017 on *L. microphyllum* plants between 2 and 3 m in height housed in the greenhouse at Florida International University. The nectar beads appeared on the petiolule, pinnule-rachises, and tertiary segments of several sterile and fertile pinnae of the *L. microphyllum* plants. Copious nectar was observed a few days later in numerous droplets present on the slightly concave adaxial surface of main rachises, along the petiolules, secondary petiolules, pinnule-rachises, and on the basal area of tertiary segments. Nectar was found on newly matured fronds with green fleshy rachises, on middle-aged fronds with gray adaxial rachis surfaces, and occasionally on very mature fronds with brown rachises and petiolules. The nectar appeared most abundant, however, on petiolules, around newly expanding leafbud apices, and along intermediate-aged rachises. The structures from which the nectar originates are not obvious and the rather uniform droplets along multiple fern parts do not appear to be associated with the uniseriate hairs previously mentioned.

Nectar collections performed throughout the day determined peak volume production to occur just before dawn. Subsequent collections of nectar for sugar concentration analyses were performed in the early mornings using a micropipette (Drummond Scientific Company, Broomall, P.A. USA), and sugar concentration of nectar was measured using a pocket sugar refractometer (0-

50%, wt./total wt. type, Bellingham & Stanley LTD. England). The sugar concentration measured ranged from 6% to 21%, but mean concentration found on mature sporophyte pinnae was 14.0% (SE = 0.9, n = 7).

The average nectar volume collected from a single pinna (from petiolule, secondary petiolules, pinnule-rachises, and tertiary segments) with active nectar secretion was 4.3 μL (max. 8.1 μL, SE = 0.5, n = 11). Nectar secretion along the rachis was also extensive, frequently occurring along its entire length between the oldest pinna and the most recently expanded, nectar-secreting pinna. At the time of these observations, no pests (scales, mites, ants, etc.) were present on any of the plants, so we are confident that the nectar present did not originate from an external source. The most noticeable nectar was visible a few days after inflicting damage by cutting back the fronds (for example, from 2 m in height down to 1 m in height) and appeared along all the surfaces previously mentioned.

Humidity in the greenhouse was high, though not measured directly. Temperatures ranged from 19°C to 36°C during the winter, and 25°C to 45°C during the summer, as logged hourly by eight thermochrons (DS1922L, Maxim Integrated, San Jose, CA) suspended around the greenhouse at mid-plant height. Light levels were measured at approximately 1 m height, at the bulk of each plant's biomass, using an Apogee quantum meter (Apogee Instruments, Logan UT). Average peak light was 297 $\mu molm^{-2}s^{-1}$ but reached as high as 600 $\mu molm^{-2}s^{-1}$. Plants were watered daily for the first year in the greenhouse, and then were transitioned into bins of water with roots partially submerged for another six months. These conditions are potentially warmer and more humid than both the native and invaded regions where *L. microphyllum* is thriving, and may contribute to this abundance of nectar production.

Previous work on the role of nectar in ferns has produced mixed results. Koptur *et al.* (2013) showed that nectar-producing fronds of an epiphytic fern, *Pleopeltis crassinervata* (Feé) T. Moore, suffered less herbivore damage than fronds on which nectaries had been covered with nail polish, which decreased activity by predatory ants. Conversely, Tempel (Ecology 64:1411–1422. 1983) observed that ants feeding on the nectaries of the bracken fern, *Pteridium aquilinum* (L.) Kuhn, provided no defensive benefits for the plant. Future work should seek to determine the composition of nectar on *L. microphyllum*, as the relative concentrations of sugars, amino acids, and other relevant compounds can provide insight into the kinds of arthropods that might be attracted (Nepi *et al.* 2009) and may indicate whether nectar production is a defensive trait in *L. microphyllum.*

The source and mode of nectar secretion must be determined, as well as whether nectar production is inducible. Future work should also consider alternative explanations for the function, or lack thereof, of nectar in *L. microphyllum*. One such explanation is the 'leaky phloem hypothesis' (De la Barrera and Nobel, Trends in Plant Science 9:65–69. 2004), which suggests that phloem solution may 'leak' as a result of increased hydrostatic pressure within the phloem, and the structural weakness of developing plant tissues. Although nectar was abundant on newly expanding leafbud apices, which could support this theory for *L. microphyllum,* it was also present on much older parts of the leaves.

Finally, it is not uncommon for multiple members of a genus to share nectar-producing traits (Weber, Porturas, and Keeler, World List of Plants with Extrafloral Nectaries. www.extrafloralnectaries.org. [accessed 9 June 2017]. 2015). Efforts should be made to determine if foliar nectar is also present on congeners of *L. microphyllum*, in particular, *Lygodium japonicum* (Thunb.) Sw., another major invasive exotic species in the southeastern USA.

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COVER CAPTION: *Cyathea oscarorum* (right), fertile pinnules, in comparison to the sympatric and highly similar *C. gracilis* (left), Montaña Negra, Cajamarca, northern Peru. Photo credit: A. Tejedor and G. Calatayud